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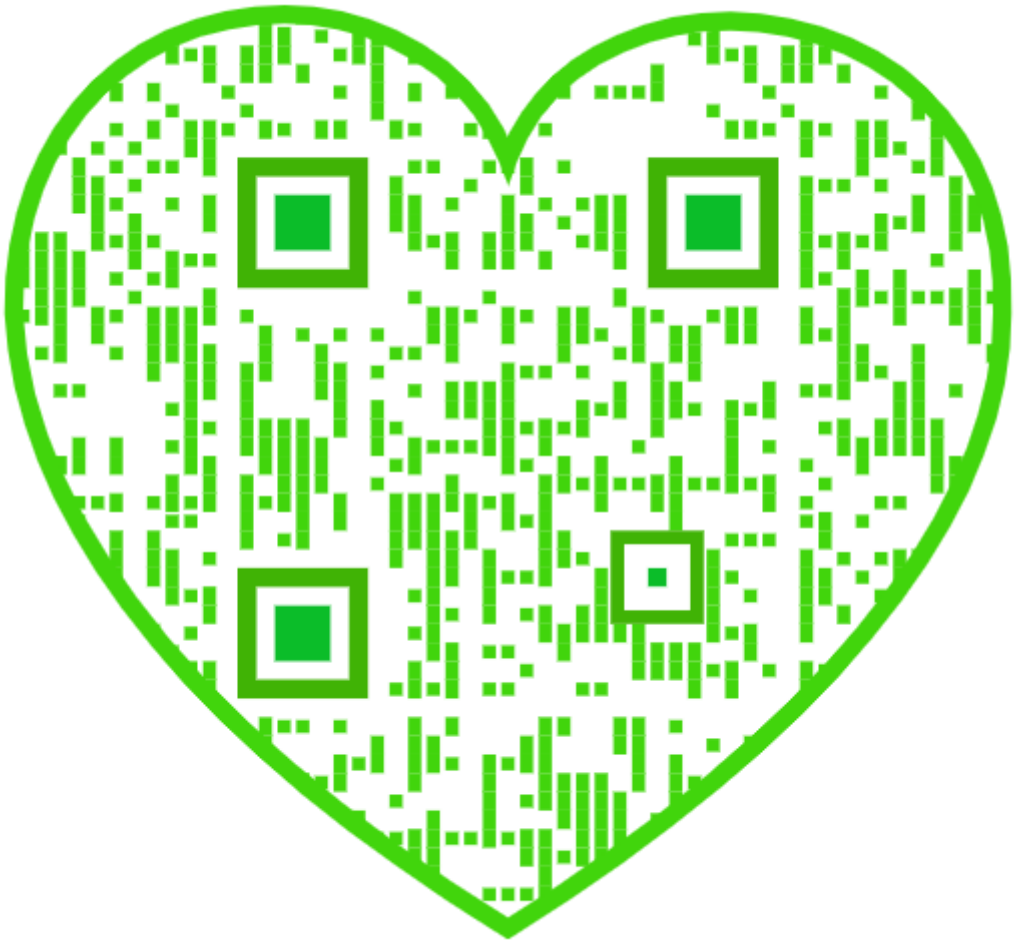

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J. Avery Shepherd.

AN INTRODUCTION

J. Avery Shepherd.

TO

BOTANY.

BY

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PREFACE.

About three centuries have elapsed since one of the earliest introductions to Botany upon record was published, in four pages folio, by Leonhart Fuchs, a learned physician of Tubingen. At that period Botany was nothing more than the art of distinguishing one plant from another, and of remembering the medical qualities, sometimes real, but more frequently imaginary, which experience, or error, or superstition, had ascribed to them. Little was known of Vegetable Physiology, nothing of Vegetable Anatomy, and even the mode of arranging species systematically had still to be discovered; while scarcely a trace existed of those modern views which have raised the science from the mere business of the herb-gatherer to a station among the branches of natural philosophy.

It now comprehends a knowledge not only of the names and uses of plants, but of their external and internal organisation, their anatomy and physiological phenomena: it involves the consideration of the plan upon which those multitudes of vegetable forms that clothe the earth have been created, of the combinations out of which so many various organs have emanated, of the laws that regulate the dispersion and location of

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species, and of the influence exercised by climate upon their development; and, lastly, from botany as now understood, in its most extensive signification, is inseparable the knowledge of the various ways in which the laws of vegetable life are applicable to the augmentation of the luxuries and comforts, or to the diminution of the wants and miseries of mankind. It is by no means, as some suppose, a science for the idle philosopher in his closet; nor is it merely an amusing accomplishment, as others appear to think; on the contrary, its field is in the midst of meadows, and gardens, and forests, on the sides of mountains, and in the depths of mines,—wherever vegetation still flourishes, or wherever it attests by its remains the existence of a former world. It is the science which converts the useless or noxious weed into the nutritious vegetable; which changes a bare volcanic rock into a green and fertile island; and which enables the man of science, by the power it gives him of judging how far the productions of one climate are susceptible of cultivation in another, to guide the colonist in his enterprises, and to save him from those errors and losses into which all such persons unacquainted with Botany are liable to fall. This science, finally, it is which teaches the physician how to discover in every region the medicines that are best adapted for the maladies prevalent in it; and which, by furnishing him with a certain clue to the knowledge of the tribes in which particular properties are, or are not, to be found, renders him as much at ease, alone and seemingly without resources, in a land of unknown herbs, as if he were in the midst of a magazine of drugs in some civilised country.

The principles of such a science must necessarily be complicated, and in certain branches, which have only for a short time occupied the attention of observers, or which depend upon obscure and ill-understood evidence, are less clearly defined than could be wished. To explain those principles; to adduce the evidence by which their truth is supposed to be proved, or the reasoning upon which they are based in cases where direct proof is unattainable; to show the causes of errors now exploded, the insufficiency of the arguments by which doubtful theories are still defended, and, in fine, to draw a line between what is certain and what is doubtful, are some of the objects of this publication, which is intended for the use of those who, without being willing to occupy themselves with a detailed examination of the vast mass of evidence upon which the modern science of botany is founded, are, nevertheless, anxious to acquire a distinct idea of the nature of that evidence. Another and not less important purpose has been to demonstrate, by a series of well-connected proofs, that in no department of natural history are the simplicity and harmony that pervade the universe more strikingly manifest that in the vegetable kingdom, where the most varied forms are produced by the combination of a very small number of distinct organs, and the most important phenomena are distinctly explained by a few simple laws of life and structure.

In the execution of these objects, I have followed very nearly the method recommended by the celebrated Professor De Candolle, than whom no man is entitled to more deference, whether you consider the soundness of his judgment in all that relates to order and arrange-

ment, or the great experience which a long and most successful career of public instruction has necessarily given him.

I have begun with what is called ORGANOGRAPHY (Book I.) ; or an explanation of the exact structure of plants ; a branch of the subject comprehending what relates either to the various forms of tissue of which vegetables are constructed, or to the external appearance their elementary organs assume in a state of combination. It is exceedingly desirable that these topics should be well understood, because they form the basis of all other parts of the science. In physiology, every function is executed through the agency of the organs : systematic arrangements depend upon characters arising out of physiological considerations ; and descriptive Botany can have no logical precision until the principles of Organography are exactly settled. A difference of opinion exists among the most distinguished botanists, upon some points connected with this subject, so that it has been found expedient to enter occasionally into much detail, for the purpose of satisfying the student of the accuracy of the facts and reasonings upon which he is expected to rely.

To this succeeds VEGETABLE PHYSIOLOGY (Book II.) ; or the History of the vital phenomena that have been observed both in plants in general, and in particular species, and also in each of their organs taken separately. It is that part of the science which has the most direct bearing upon practical objects. Its laws, however, are either unintelligible, or susceptible of no exact appreciation, without a previous acquaintance with the more important details of Organography. Much of the subject

is at present involved in doubt, and the accuracy of some of the conclusions of physiologists is inferred rather than demonstrated; so that it has been found essential that the grounds of the more popularly received opinions, whether admitted as true or rejected as erroneous, should be given at length.

Next follows GLOSSOLOGY (Book III.); or, as it was formerly called, TERMINOLOGY; restricted to the definition of the adjective terms, which are either used exclusively in Botany, or which are employed in that science in some particular and unusual sense. The key to this book, as also to the substantive terms explained in Organography, will be found in a copious index.

It has been my wish to bring every subject that I have introduced down, as nearly as possible, to the state in which it is found at the present day. In doing so, I have added so very considerable a quantity of additional matter, especially in what relates to Vegetable Anatomy and Physiology, that the present edition may be considered, in those respects, a new work.

In the course of the following pages I have made frequent use of many valuable translations to be found in the *Annals of Natural History*, a periodical of the highest merit, to which all naturalists should have access. In every case it has been my anxious wish to render credit to all persons for their discoveries; and if I have on any occasion either omitted to do so, or assumed to myself observations which belong to others, it has been unknowingly or inadvertently. It is, however impracticable, and if practicable it would not be worth while, to remember upon all occasions from what particular sources information may have been derived.

Discoveries, when once communicated to the world, become public property: they are thrown into the common stock for mutual benefit; and it is only in the case of debateable opinions, or of any recent and unconfirmed observations, that it really interests the world that authorities should be quoted at all. In the language of a highly valued friend, when writing upon another subject:—"The advanced state of a science is but the accumulation of the discoveries and inventions of many: to refer each of these to its author is the business of the history of science, but does not belong to a work which professes merely to give an account of the science as it is: all that is generally acknowledged must pass current from author to author."*

* Brett's Principles of Astronomy, p. v.

London,
June, 1848.

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INTRODUCTION

TO

BOTANY.

PRELIMINARY.

Botany is the Science which treats of Plants.

A plant is a cellular body, possessing vitality, living by absorption through its outer surface, and secreting starch.

This is a definition to which, in the existing state of knowledge, there seems to be no objection. Others define a plant differently.

Linnæus distinguished a plant from an animal by its growing and living without consciousness (*Vegetabilia crescunt et vivunt.* Animalia crescunt, vivunt et *sentiunt*); and he abandoned the old differences of locomotion and local nutrition which were supposed to be peculiar, the first to animals, the second to plants. Both Jungius and Boerhaave defined a plant to be a living body, attached to another body by some part of itself, through which part it obtains and attracts the materials for nutrition, growth, and life. Ludwig regarded the power of locomotion in animals as their sole distinction from plants. But it is impossible to deny the power of locomotion to Brittleworts (*Diatomaceæ*) or young Algals (see *Lindley's Vegetable Kingdom,* p. 14). Multitudes of aquatic Thallogens are produced and nourished without any fixed point of attachment, and when motion has all the appearance of being

spontaneous, as in the plants just mentioned, the denial to them of the same degree of consciousness as is supposed to exist among the infusorial animalcules is a hypothesis unsupported by evidence.

Mirbel was of opinion that plants cannot be distinugished from animals by any positive character (*Elémens de Physiologie Végétale*, p. 17), but that they form two graduated series, starting from a common point. He more especially objected to the denial of consciousness to plants. "Let us take the Polype," he observes, "a production the least morsel of which produces a new individual. How are we to determine whether such beings, which indicate no trace of organs of sensibility, possess the power of perception? We see indeed that they move, catch small insects, and seem to select their food; but certain plants, to all appearance, behave in the same manner. Can we deny the faculty of sensation to the Sensitive or the Dionæa, and yet maintain the presence of this noble attribute among zoophytes? In this matter we have no other guide than analogy. On the one hand, because zoophytes move in the very same way as animals manifestly provided with nerves and muscles, we assume that their motions have the same origin; and on the other hand, finding that the few plants which move like sentient beings have nevertheless the greatest resemblance in form, organisation, and development to other plants, which, according to our notions, have no sensibility, we infer that the movements of the last depend upon mere organic contractibility, independent of volition and sensation. To this point only goes the intelligence of man in such delicate questions." If in the year 1815, when this passage was written, doubts could thus be raised as to the absence of all traces of perception among plants, the argument of Mirbel has become strengthened into conclusiveness now that the habits of plants are better understood.

Link defines a plant to be an organised body, nourished from without, while animals receive their food from within. But he observes that there are vital actions in which the nutrition of plants and animals is the same, as in the progressive development of the ovule; "at that point plants

acquire an internal animal life, which they sooner or later lose again:" that is to say, during the early formation of the plant in the ovule, it is nourished from within like an animal, and not from without like a vegetable.

De Candolle distinguishes plants from animals by their want of voluntary motion and of a stomach, with both which animals are provided. This definition is open not only to the objection that many plants move with as much appearance of consciousness as some animals, but that a plant is in reality an organised body composed of many stomachs; for, in a physiological sense, every vegetable cell is a stomach.

Plants, says Achille Richard, are organised and living beings which attract from the atmosphere, the water, or the soil, in a word, from the media in which they are placed, the food required for their support and growth, and which are reproduced by bodies growing either on their external surface or their interior. But this definition obviously includes the whole race of infusorial animalcules.

The definition of Endlicher (*Grundzüge der Botanik*, p. 1), namely, that living beings which grow and reproduce themselves, but which can neither move spontaneously nor feel, are called plants, is merely hypothetical. Nevertheless it is also that of Adrien de Jussieu. (*Cours Elémentaire*, p. 1.)

As to the description of a plant given by Oken, it is obviously, notwithstanding its diffuseness, destitute of everything like distinctness or precision, and tinctured with all that mysticism which renders his writings so repulsive to sober minds.

"The plant," says this philosopher, "is an organic body chained to the earth; it is only developed out of water, and in the dark, in the earth; is associated with metal, and carbon; is a magnetic needle attracted out of earth into air towards light. Seeds germinate better when guarded from the access of light; the radicle sinks, indeed, into the earth, because it obeys gravitation and rest; but it is maintained there, because the earth is moist and dark. This is a reason for a plant being chained to the earth, not enough adverted to. Some plants, indeed, take root in water, but water is darker than air. The root has, in this respect, completely the

character of metal, which is a child of darkness."—(*Naturphilosophie,* 1040, ed. 3.)

Scarcely less objectionable is the assertion of Dr. D. P. Gardner, who declares (*Philosophical Magazine and Journal of Science,* vol. xxviii., p. 432) "the physical structure of plants to be that of a porous system subject to the laws of the diffusion of gases and endowed with no vitality other than the power of forming cytoblasts and arranging cellules after a definite type." So that it would seem as if the singular phenomenon of impregnation, the invariable directions assumed by organs, the infinite diversity of forms, colours, and attributes belonging to plants, their irritability, their locomotion, such as it is, all which are inexplicable by the laws of chemistry, electricity, or physics, were mere phenomena belonging to a "porous system" of any sort. If this were so, Dr. Gardner should be able to make a plant and set it in action. Can he do that?

Upon the whole, it seems impossible to define a plant without taking into account the power which all vegetables possess of secreting starch, a power unknown in the animal kingdom. This property has been shown by M. Payen to exist in those heretofore doubtful bodies, which former naturalists referred to Corallines, but which M. Decaisne has proved to be truly plants.

The former observes (*Ann. des Sciences Nat.,* 2d ser., xx. 67), "that although the results at which he had arrived seemed perfectly conclusive as to the vegetable nature of calciferous Corallines, he nevertheless thought it would be as well to seek in the tissues of Corallina the properties which, in addition to its elementary composition, characterise cellulose, the immediate principle that binds together every vegetable structure, and is the chief constituent of the membranes of plants. For this purpose he took a piece of Corallina officinalis, treated it with dilute muriatic acid to get rid of the incrustations, washed it, then treated it with ammonia, again washed it and placed it with a little tincture of iodine between two plates of glass under the microscope; all the quaternary substances contained in the cells or which had penetrated their sides immediately became tinged orange-yellow. After

this preparation, he introduced between the plates of glass a drop of sulphuric acid (1 eq. of acid being mixed with 4 eqs. of water), and he was then able to follow the process of disaggregation which marked the arrival and passage of the acid; an orange tint, brown next the tissue which contained quaternary substance in abundance, was first visible; then in the rest of the tissue were seen the first dissolving reactions finishing the effect of the tincture of iodine; the cellulose became gradually divided into groups of amylaceous particles, which gave a beautiful violet-coloured outline to the cylindrical cells radiating or spread out symmetrically from the points of insertion of each joint."

BOOK I.

ORGANOGRAPHY; OR, OF THE STRUCTURE OF PLANTS.

CHAPTER I.

OF THE ELEMENTARY ORGANS.

If plants are considered with reference to their internal organisation, they appear at first sight to consist of a vast multitude of exceedingly minute cavities, separated by a membranous substance; more exactly examined, it is found that these cavities have a variety of different figures, and that each is closed up from those that surround it; if the inquiry is carried still farther, it will be discovered that the partitions between the cavities are all double, and that by maceration in water, or by other methods, the cavities with their enclosing membrane may be separated from each other into distinct bodies. These bodies constitute what is called Vegetable Tissue, or Elementary Organs: they are the *Similary parts* of Grew.

The organic basis of the elementary organs is called *cellulose*, a ternary compound, derived from *cambium* or *organic mucus*, a viscid azotised quaternary secretion, which occurs everywhere in young parts, and as a residuum in old parts. This organic mucus, or cambium, is also named, by Vegetable Physiologists, *organisable matter*.

Organic mucus has long been known as a substance existing in Algals, prior to the appearance of organisation, as in Protococcus nivalis, &c. It has been found by Brongniart, Henslow, &c. in the form of cuticle, a thin homogeneous

membrane, applied to the surface of the leaves of some plants, and only separable after maceration; it is probable that it constitutes the whole exterior coating of all plants; it is certainly drawn over the sacs which constitute hairs; I have found it distinctly on the petals of Hydrotænia Meleagris (see *Bot. Reg.* 1838. misc. No. 128), but its extreme tenuity and firm adhesion to the tissue below it renders it difficult to detect it; and there is no doubt that it occurs very generally in the interior of plants between their cells, filling up the intercellular spaces, and gluing together all the parts. Mohl, with his usual skill, has shown that this substance is found so frequently, that we cannot refuse to acknowledge its presence as a constant fact. The Box, and the young annual shoots of Sambucus nigra, are especially noticed as well suited to show this structure; it will be seen to form a considerable part of the mass of the albumen of Alstromeria Salsilla, see fig. 2. *c.* where it is $\frac{1}{3500}$ of an inch in diameter. Valentin has measured the thickness of the intercellular organic mucus in several instances, and gives the following table of the proportion between it and the cells of certain plants, calculated in Paris inches.

	Thickness of the intercellular mucus.	Size of the cell.	Proportion of the 1st to the 2nd.
Camellia japonica . .	0,000112	0,000675	1 : 6,02
Hoya carnosa . . .	0,000150	0,000650	1 : 4,33
Magnolia grandiflora .	0,000150	0,000425	1 : 2,83
Cestrum laurifolium .	0,000275	0,001550	1 : 5,63
Daphne Laureola . .	0,000390	0,001000	1 : 2,56
Pinus Picea . . .	0,000450	0,001200	1 : 2,66
Aloe intermedia . . .	0,000775	0,002100	1 : 2,71
Aloe Lingua . . .	0,000825	0,002575	1 : 3,12
Agave americana . . .	0,000850	0,002375	1 : 2,79

Meyen admits the fact of the presence of this intercellular mucus, and considers it a secretion from the sides of the cells. He particularly refers to its condition in the petiole of Beta cycla, in proof of the correctness of that view.

No doubt can be entertained that it is of universal occurrence between the cells or tubes of all vegetable fabrics.

Cambium, as it is called, originally observed at the separation of the bark and wood of Exogens, in the spring, seems

to be nothing more than this universally distributed organic mucus. An account of its composition and of the part which it plays in the Vegetable Organisation, has been given by Mirbel and Payen, (*Comptes rendus*, 1843, i. 98; *Annales des Sciences Nat.*, xix. p. 193). They describe this substance, which precedes the appearance of cells, and is always present where vegetable matter is in a state of growth, as containing substances analogous to those which constitute animal bodies, that is to say, including nitrogen. It is, however, also mixed with other materials not azotised, composed of carbon and the elements of water, such as dextrine, gum, starch, sugar, glycose, mannite, &c. At the moment when vegetation is renewed by the development of cells, unazotised cellulose also appears, and increases by new layers, identical in their chemical constitution, although sometimes other matters are added to form woody tissue. From this kind of thickening of cellulose, we can understand, say our authors, why wood in the interior of stems contains little nitrogen, while spongioles, buds, and growing ovules, contain from ten to twenty times as much. It may be, however, that, as Link says, the word cambium is applied by Payen and Mirbel to secretions essentially different, and that much more refined chemical analysis is required to show that all intercellular or organisable matter is identical in composition.

It is the opinion of some anatomists that of membrane and fibre, the latter only is the basis of the tissue of plants: fibre itself being a form of membrane; or, which there is no sufficient evidence to show, that all membrane is composed of fibres interlaced. But we find both the one and the other developed in many of the most imperfectly organised plants, such as Scleroderma and other fungals, and it is difficult to conceive how that can be a mere modification of membrane which can be generated independently of it, which has no external resemblance to it, and which in most cases is obviously something superadded. Link observes that Mohl has taken great pains to refute Meyen's assertion, that the vegetable membrane is formed of spiral fibres. But in reality the assertion had only a very limited application, because by far the greatest number of membranes in the

vegetable kingdom do not exhibit such a composition. Link never could find the spiral structure described by Meyen in the aerial roots of what he calls a Stelis. It is, however, very remarkable, as Link observes, "that many portions of plants have a tendency to split spirally; this, however, only takes place in the thicker parts; for instance, in old porous vessels, and even in bark, as in that of the birch tree. We need not, therefore, go back with Mohl to a molecular theory, which is better left to the 'philosophers' of nature." (See p. 13.)

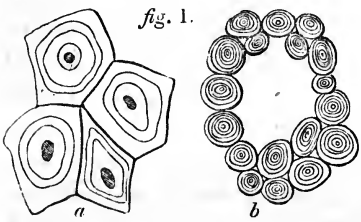
Membrane, as true cellulose, may be regarded as being in the beginning a gelatinous precipitate from the organic mucus of vegetation. Like all such precipitates, it must be understood to be a collection of globular molecules adhering by their points of contact; and hence its permeability. The history of organic precipitates has been studied by both Harting and Link, of whom the latter thus states the result of his observations:—"All precipitates, when analysed immediately after their formation, exhibit globules; these globules unite themselves to larger ones (being therefore fluid, like globules of quicksilver); and these united globules or drops, subsequently only (and that frequently under our own eyes) change themselves into crystals. If M. Harting did not observe this, it was owing to his not having examined the precipitates speedily enough. The globules sometimes form flat surfaces, sometimes they are gelatinous. All fluid substances exhibit a commencement of solidity on their surface—for we attribute fluidity to a substance, if the parts can be displaced from each other by the slightest application of force; and this can only be done, when the attracting and repelling powers of the homogeneous parts neutralise each other, which cannot be the case on the surface of fluid substances, where the parts are unequally drawn in different directions. This solidity increases with the surface, and a thin stratum of fluidity is consequently in itself solid. The degree of solidity certainly depends on the degree of attraction among the parts, which, as is well known, is different also in fluid substances, as exhibited by quicksilver and water. Nothing, therefore, is required for the production of a

membrane, but the separation of a stratum of fluidity—as every bubble shows. The half fluid substances, mucus, jelly, &c., are a mixture of solid and fluid parts, as can be seen when they are dried."

Membrane varies in its degree of transparency, being occasionally so exceedingly thin as to be scarcely discoverable, except by the little particles that stick to it, or by its refraction of light, but in ferns, some fuci, and other cryptogamic plants, it is brown from its first birth: according to Röper it is green in Viscum album: Link says it is green in the leaves of Ruellia Sabiniana and the petiole of Cycas revoluta; and Meyen mentions its being orange-coloured in the petiole of many tropical Orchids.

It is always excessively thin when first generated; and whatever thickness it afterwards acquires must be supposed to be owing to the incorporation or incrustation of secreted matter. This was first observed by Mohl in Palm-trees, where he found a successive addition of strata to the lining of the cavities of the cells; and is apparently an universal occurrence where membrane becomes thickened. But the matter added to membrane is often so homogenous as to offer no trace of its being deposited concentrically, even when examined by the most powerful microscopes, and I am not always able to discover the regular lines upon its section which are represented so uniformly by the German anatomists. It is, however, plain enough that the membrane of the woody tubes of the liber is in many plants thickened successively by the deposit inside of concentric layers of sedimentary matter, as may be seen in Castanea vesca (*fig.* 1. *a*), and Betula alba, and in the cells below the stomates of Pinus sylvestris (*fig.* 1. *b*); and there are sufficient traces of it to be found elsewhere to justify the opinion that it is a common mode of increment in thickness.

fig. 1.



The first layer of matter is invariably soft and azotised, and now bears the well-contrived name of *protoplasm*, proposed

by Professor Mohl. Turpin has remarked that the thickening of the membranous sides of cells by means of a hard sedimentary matter, called by him *Sclerogen*, is what causes the grittiness of the pear, and the boniness of the stone of the peach and plum, in all which the osseous parts were originally membranous. It is, however, by no means in old or woody parts alone that a thickening of the membrane takes place: it may be observed distinctly in the cells of the corolla of Convolvulus tricolor, and in fact occurs in all parts containing fluid matter exposed to vital action.

Mohl and others are of opinion that all addition to the thickness of vegetable membrane takes place on its inner face; but the universal presence of a cuticle overlying the outer series of cells in every organ exposed to air, and the granulations found on the outside of old hairs (see *Elements of Botany*, fig. 67), render it difficult to deny the increment of membrane in thickness on both sides. This view has more especially been taken by Harting and Mulder, who conclude from chemical evidence, that in the development of cell-membrane, all the layers which in a full-grown cell have a peculiar chemical reaction not occurring in the young membrane, have been formed subsequently to that membrane, which consists entirely of cellulose; and that since such layers occur on the outside of full-grown cells (the innermost layer of which is composed of cellulose, and therefore corresponds to the membrane of the young cell), the cell-membrane must have increased in thickness in consequence of a subsequent deposition, from within outwards, of layers having a different chemical constitution. Mohl has discussed this opinion with his usual sagacity. "Let us examine," he says, "whether these conclusions may not be too hasty. It does not admit of the slightest doubt, that the chemical compounds which are coloured yellow by iodine and sulphuric acid, and which characterise the outer and intermediate layers of most full-grown cells, are of later origin than the cellulose which forms the membrane of the young cell. From this fact, however, it is a great leap to the assumption, that those layers which are composed of a substance differing from cellulose, are in reference to their situation also newly-formed layers,

such as are wanting in young cells. That is certainly possible; but it is also possible, that the fact as shown by anatomy is altogether otherwise. With the same kind of reason as that which leads to the inference that a new layer is formed externally, we may assume that in a cell originally consisting of true cellulose, that substance subsequently, and without any alteration of its relative position, is absorbed and replaced by an essentially different chemical compound; or that cellulose remains and a new compound is deposited between its molecules, interfering with the behaviour of cellulose towards iodine and sulphuric acid. Such an infiltration might occur without any visible thickening of the layer, either if it were not in very great abundance, or if the growth of the membrane in a lateral direction, in consequence of the expansion of the cell, were to make room for the deposit of a considerable quantity of some foreign compound. In these cases, the possibility of which no one will call in question, a layer would indeed be formed altogether new in a chemical aspect, but no alteration in anatomical relations would appear: and from such a chemical transformation no conclusion should be drawn as to the order in which the different layers of the cell-membrane originate; because such metamorphoses may take place as readily in the last as in the first formed layer. If we admit the possibility of such a metamorphosis, it must also be conceded that the chemical reaction of any particular layer affords no sure means of recognising it as a peculiar anatomical layer; for it may be easily imagined, that in different cells, the layers corresponding to each other in an anatomical point of view, may exhibit a great distinction in regard to their chemical transformations. Until well-grounded experience has taught us which of the cases, that have here been mentioned as possible, really occurs in nature, we can only allow ourselves to be guided, in the recognition of the different layers and the determination of the order in which they make their appearance, by their anatomical relations; and although in very many cases the influence of chemical re-agents affords an excellent means by which we are enabled to distinguish the individual layers of cell-membrane, which without this

assistance it would be difficult or impossible to recognise, yet in availing ourselves of such assistance we must keep the anatomical relations constantly in view. The study of these relations leads, I believe, to a result diametrically opposed to that maintained by Mulder and Harting. (See *Annals of Natural History*, vol. xviii., p. 265, for further details.)

Elementary membrane generally tears readily, as if its component atoms did not cohere with greater force in one direction than another; but I have met with a remarkable instance to the contrary of this in Bromelia nudicaulis, in which the membrane of the cuticle breaks into little teeth of nearly equal width when torn. (Plate I. fig. 6.) The same circumstance has been remarked by Dr. Willshire in Tillandsia usneoides. (*Ann. Nat. Hist.* xviii.) Hence it may be conjectured, that what we call primitive membrane is itself the result either of primitive fibres completely consolidated, or of molecules originally disposed in a spiral direction, as Raspail supposes. (*Chim. Org.* p. 85.) In the membrane of certain plants, as in the liber of the Oleander, in Vinca minor, and others belonging to the families of Dogbanes (Apocynaceæ) and Asclepiads, an appearance is discoverable of spiral steep ascending lines, some of which turn to the right, others to the left, thus dividing the surface into a number of minute rhomboidal spaces. Mohl, however, who has made this observation, does not therefore consider with Grew that the membrane is woven together of fibres, but that their appearance is owing to a small difference in the thickness of the cellular membrane: "Perhaps a different arrangement of the molecules at various points, perhaps a small difference in the thickness of the membrane, causes a different refraction of light, precisely in the same way as fibres are visible in badly melted glass." Valentin confirms Mohl's views, and regards such appearances as caused by the process of lignification. Schleiden goes further, and maintains that all the deposits to which the thickening of membrane is owing have originally a spiral direction. (See p. 9.)

Membrane is in all cases, when first formed, destitute of visible pores; although, as it is readily permeable by fluids, it must necessarily be furnished with invisible passages. An

opinion to the contrary of this has been held by some botanists, who have described the existence of holes or pores in the membrane of tissue, and have even thought they saw a distinct rim to them; but this idea, which originated in imperfect observation with ill-constructed glasses, is now generally abandoned. (See p. 16.)

Different explanations have been given of the supposed pores. Dutrochet asserted them to be grains of matter sticking to the membrane: he found that boiling them in hot nitric acid rendered them opaque, and that treating them with a solution of caustic potash restored their transparency,—a property incompatible with a perforation. But the so-called pores operated upon by this observer were particles of some secreted matter sticking to the membrane. Slack believed them to be, in other cases, thin spaces in the sides of tissue, such as might be produced by the adhesion and separation at regular intervals of a thread developed spirally within a membranous sac. (*Trans. Soc. Arts,* xlix.) A nearly similar opinion was previously offered by Mohl, who considers the dots on the membrane of tissue to be thinner portions of it. He says it may be distinctly seen by the aid of a powerful miscroscope that the little circles which are visible on the surface of the tissue of Palm-trees are passages (*meatus*) in the thickness of the membrane, opening into the cavity of the cells, and closed externally by the membrane itself. He adds, that when dotted tissue is in contact, these passages are placed exactly opposite to each other. (*Martius Palm. Anat.* v. *col.* 2). To the latter cause is undoubtedly owing the general appearance of dots, as has now been ascertained by repeated observations. If a thin section of any vessel or cell, the sides of which appear to be dotted, is placed under a good microscope, it will be found to have the matter deposited on its sides pierced with short passages, which give the appearance of dotting, because the sides of the membrane are thinner where they are stationed than anywhere else. (See Plate II. fig. 2.) They are therefore not dots, but *pits*.

Should the young observer fail in seeing the pits in their natural state, the application of tincture of iodine to the subject under examination will enable him to discover them

readily, with a magnifying power of 350 diameters. But it is by no means to thin transparent tissue that these passages are confined; they are universally present in the sides of the thickest sided tissue, where they form minute *cul-de-sacs*, often branched, and always opening into the interior of the cell. They may be readily found in the gritty tissue of the pear (*fig.* 2. *a*), the stone of the plum *b*, and the compact albumen of seeds. *Fig.* 2. *c* represents them in the albumen of Alströmeria, where they are about $\frac{1}{7500}$ of an inch in diameter.

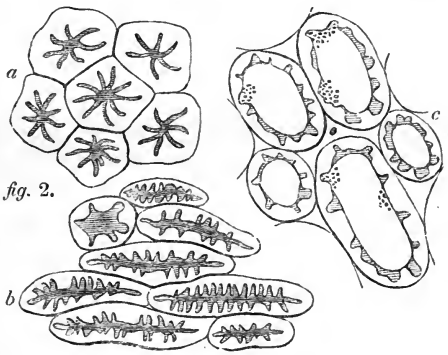


fig. 2.

By what power the sedimentary matter, left on the sides of such tissue as this, is prevented from choking up the pits, is at present unknown.

It is, no doubt, very common for the pits of the membrane of one cell to be placed exactly opposite those of the next cell, as is seen in the irregular half-gelatinous tissue of Cereus grandiflorus (see Plate II. fig. 1. *a a*), so that it may be supposed that they are passages to allow of permeation from one cell to another; but this arrangement is by no means uniform (see same fig. *b*).*

The absence of pores from vegetable membrane has been so generally admitted, that it would have seemed needless to insist upon the erroneous notions of the old anatomists, had not two recent observers, Harting and Mulder, revived the question by asserting that, almost universally, the yet

* For the supposed chemical difference between elementary membrane and fibre, see Book II. Chapter I.

unthickened membrane of young cells, when coloured blue by iodine and sulphuric acid, is seen to be perforated like a sieve by a great number of small pores, through which the light appears bright and uncoloured; the cells of the pith of Asclepias syriaca, Hoya carnosa, Ricinus communis, of the bark of Euphorbia Caput medusæ, of the wood of Asclepias syriaca, and Clematis Vitalba, are especially named in relation to this. Harting states that in the old medulla-cells with thickened walls of a great many dicotyledonous trees, *e. g.* Æsculus Hippocastanum, Syringa vulgaris, Rosa canina, Sophora japonica, there are, among the canals of the dots closed by a membrane, others which are quite open; and from his investigations he was led to the conclusion that these open pores are not the result of the absorption of the membrane closing the canal, but that they are really remains of pores occurring in the young cell, which have not, like the others, become closed at a subsequent period. (*Annals of Natural History*, xviii. 146.) Mohl's reply to this seems conclusive—"I had already," says this admirable phytotomist, "in cells coloured blue by iodine, often seen very bright dots, which appeared like real orifices, but I always believed that I saw a closing membrane; yet as I might have been deceived in my earlier observations, I submitted this to a new investigation. In the first place, however, I must remark that I do not wholly approve of the mode of examination with iodine and sulphuric acid, chosen by Harting and Mulder; a deep blue colouring of the young cell-membrane is indeed obtained by this means, but in fact this deep colour is not advantageous, as will hereafter appear; moreover, when too strong an acid is employed, a considerable expansion of the cell-membrane is readily caused, by which the dots may be closed; this indeed cannot give rise to a delusion in reference to the presence or absence of a closing membrane, but renders the making of a new preparation necessary. Both evils are avoided when no sulphuric acid is used; but the cell-wall is coloured blue by the application of very concentrated tincture of iodine, and subsequent moistening with water. In this way we are not exposed to the risk of producing a mechanical alteration of the cell-membrane, and

there is the further advantage, that the preparation coloured by iodine may be allowed to dry again, by which means, as is known, the detection of a very thin and transparent membrane is especially facilitated. I treated in this way the medulla-cells of the young developing bud of Sambucus nigra, Asclepias syriaca, and of the apex of the stem of Euphorbia Caput medusæ. The result of the microscopical examination of these does not at all agree with that offered by Harting and Mulder. It is certainly quite true that dots are so transparent, and appear so bright in the coloured cell-membranes, especially when they have acquired a deep indigo tint, that by an illusion they look like true openings. But to make the fact certain, we must ascertain accurately the performance of our microscope, and carefully select a suitable objective, and a covering glass of proper thickness must regulate the proper illumination; in short, we must neglect no circumstance which may influence an important microscopical examination. Since the question, whether in these young cells actual openings are present or not, is one of the principal hinges on which the doctrine of the development of cell-membrane turns, I may be permitted to enter somewhat minutely into the qualifications of the microscope employed by me in these investigations. I am, indeed, generally speaking, of opinion that the accuracy of a microscopical observation does not depend upon the fact of the microscope being a little better or worse, since experience in observation frequently counterbalances the inferiority of the instrument; but I consider that the present case is one of those in which an instrument of the most superior quality is necessary, and in which we cannot come at the truth without a microscope of great penetrating power. I commonly make use, in important investigations, of the three strongest of Plössl's objectives, (No. 5—7), with an Amici's achromatic ocular, since this combination gives an image of surpassing sharpness and clearness, with a magnifying power of about 300. Notwithstanding the superior performance of this combination, I was never in a condition to detect any trace of a membrane closing the dot in the young medulla-cells of Sambucus, since the light shone through perfectly bright and clear,

and apparently quite uncoloured as through a true opening. But when I used the strongest of Amici's objectives, which can only be employed advantageously in a few cases, and to very delicate and transparent objects, but which, with the same ocular, gives a magnifying power of 500 diameters, every doubt was dissipated as to whether a membrane was stretched over the dot or not, since such a membrane was now plainly to be perceived: it was, indeed, very transparent, but small granules, &c., were distinctly to be seen adhering to it. If this was not to be mistaken in the preparation which was lying in water, the result of the examination of dried preparations was yet more decisive, since no doubt was longer possible as to the presence of a closing membrane, and of the bright violet colouring of the same." Mohl then goes into a variety of evidence in support of the general opinion that membrane is originally imperforate, for which the reader is referred to the excellent translation of his paper in the *Annals of Natural History*, vol. xviii. p. 148. It will, however, be hereafter seen that full-grown cells are occasionally pierced by loop-holes of such considerable diameter as to permit the passage of animalcules through them. (See page 46.)

Elementary Fibre may be compared to hair of inconceivable fineness, but it is extremely variable in size. In Pleurothallis ruscifolia, where it is large, I find it $\frac{1}{3000}$, in Crinum amabile, where it is middle sized, $\frac{1}{7250}$ of an English inch in diameter. It has frequently a greenish colour, but is more commonly transparent and colourless. It appears to be sometimes capable of extension with the same rapidity as the membrane among which it lies, and to which it usually adheres; but it occasionally elongates less rapidly, when it is broken into minute portions, and is carried along by the growing membrane. In direction it is variable (Plates I. and II.); sometimes it is straight, and attains a considerable length, as in some fungals; sometimes it is short and straight, but hooked at the apex, as in the lining of the anther of Campanula; occasionally it is straight, and adheres to the side of membrane, as in the same part in Digitalis purpurea; but its

most common direction is spiral. Whether it is solid or hollow has been disputed; Purkinje asserts that it is hollow, but there can be no doubt that it is really solid, as it is believed to be by the best anatomists, and as its mode of formation indicates. Elementary fibre has a constant tendency to anastomose, in consequence of which reticulated appearances are frequently found in tissue. Slack adds that it sometimes branches. Like membrane it is increased in thickness by the deposit of sedimentary matter on that part which does not adhere to the membrane, as has been proved by some beautiful microscopico-chemical experiments of Schleiden.

In its most simple state the elementary fibre forms a loose spire coiled up in the interior of cells, with a thickening at one end derived, according to the opinion of Nägeli, from a nucleolus (see *postea*), tapering to a point at the other, having an active vermicular motion when extricated from the cell in water, and losing the motion at the instant when it is acted upon by iodine. Such loose spires are common in the antheridia of mosses and liverworts where they were first noticed; they have since been found in the young leaves of ferns and elsewhere. The early observers of them supposed them to be animalcules analogous to the genus Vibrio; and Grisebach, who took this view of their nature, called them *phytozoa*, and detected them elsewhere, giving the following account of them. (See *Annals of Natural History*, vol. xv. p. 265.)

"The occurrence of phytozoa in organs of vegetation, led me to expect that they might be detected in Phænogamous plants. I had frequently observed in the water on the glass stage, while examining leaf-buds, masses of dark particles, which, on being magnified 200 times, exhibited a lively vermicular motion. On recently re-examining them in the buds of Rhamnus infectorius and pumilus, I saw distinctly, with a magnifying power of 410, that they were phytozoa, accurately agreeing with those in ferns. Like them they consist of long-tailed globules which are individually inclosed in a very minute spherical cell, or swim freely about in the water, oscillate in a lively manner, and sometimes move their tail."

The part of the Rhamni in which these loose vermicular spirals were observed are certain obovate bodies belonging to the nascent stipules of the leaf-buds.

The frequent occurrence of such a structure in very young organs, the loose fibres found in the hairs of the seeds of Collomia, and other plants, in the elaters of Marchantia and elsewhere, would seem to render the independent nature of the elementary fibre unquestionable, notwithstanding its more frequent adhesion to the inside of some cell or tube in which it is generated. Nevertheless Mohl says (*Botanische zeitung*, vol. xxii. p. 676,) "No doubt can be entertained by any one, who has investigated the development of the spiral fibres and the spiral cells, and who has recognised the decided analogy between these two formations and dotted cells, that the fibre of the spiral vessels is no peculiar formation, existing by itself, but that it must be considered as the secondary membrane of the vascular sac, having a spiral direction, and divided into one or several parallel bands." But I agree with Link in asking whether the membrane was connected with the fibre at the moment of its first formation, or whether a separation into fibres only takes place subsequently? "I shall demand proofs if this question is answered in the affirmative; and if in the negative—if the fibre is assumed to be separated from the membrane immediately at its first formation—I shall then ask further, What difference is there in saying, the fibre is a peculiar independent tissue; or, a membrane is peculiar, and primitively separated into fibres? The word 'depositing' does not explain anything; on the contrary, it has the improbable unproved meaning, that the formation of the fibre and of the membrane was a mere act of precipitation. Even when fibre is pressed rather flat, it has no similarity with the parts of a membrane; for, on magnifying 1500 times tissue from very young roots, the tender fibres of the spiral vessels may distinctly be seen rounded on the edges. The inclosing external membrane at that period being so tender, that it cannot be perceived, I should like to reverse the matter and to say, Whoever investigates the development of spiral vessels and of spiral cells,

must acknowledge the fibre to be a peculiar independent formation." (See *Link's Report upon the Botany of* 1841, as translated for the Royal Society by Dr. Lankester.)

Of the organic mucus, membrane, and elementary fibre thus described, all the elementary organs of plants are constructed. For the convenience of description, they may be considered as of five different kinds, 1. *Cellular tissue,* or *Parenchym;* 2. *Pitted tissue,* or *Bothrenchym;* 3. *Woody tissue,* or *Pleurenchym;* 4. *Vascular tissue,* or *Trachenchym;* 5. *Laticiferous tissue,* or *Cinenchym.**

There is no doubt that all these forms are in reality modifications of one common type, namely, the simple cell, however different they may be from each other in station, function, or appearance. For, in the first place, we find them all

* Professor Morren has proposed the following nomenclature of tissue, which has some advantages over that more commonly in use. I. PARENCHYMA; 1. *merenchyma,* or *sphærenchyma,* spherical; 2. *conenchyma,* conical, as in hairs; 3. *ovenchyma,* oval; 4. *atractenchyma,* fusiform; 5. *cylindrenchyma,* cylindrical; 6. *colpenchyma,* sinuous; 7. *cladenchyma,* branched; 8. *prismenchyma,* prismatical. II. PERENCHYMA, amylaceous granules. III. INENCHYMA, fibro-cellular tissue. IV. ANGIENCHYMA, vascular tissue; 1. *pleurenchyma,* woody tissue; 2. *trachenchyma,* spiral vessels; 3. *modified trachenchyma,* ducts; 4. *cinenchyma,* laticiferous vessels.—Count de Tristan distinguishes tissue into several kinds. Common spheroidal tissue is for him *aphrostase,* because it resembles foam. Prismatical cellular tissue is *hegemon.* A division, or fissure, which he calls "*cunice,*" separates, in trees, the bark from the internal part, or "*endophyte*" as he terms it. The inner part, however, does not consist of a single part, but of the pith, and that which is called wood, but which does not always deserve this name, as it is frequently very soft in herbs. Count de Tristan therefore terms it "*endostere,*" because it is at all events firmer than the surrounding part. As to the so-termed "*prolongemens medullaires,*" he says that they originate from the "*tissue aphrostasien,*" that they continually get smaller, and that the vascular bundles which have grown up, thicken, at last only leaving a trace of them. He therefore terms them "*isthmes aphrostasiens,*" or briefly "*isthmes.*" The consideration of a transverse section in the stem of a bramble (*Rubus fruticosus*) leads him to the adoption of a third tissue, which he terms "*proxyle,*" distinguishing it by the circumstance, that it consists of prismatic or cylindrical fibres (filets) of an indefinite length; this is the woody tissue of liber. He examines it from its first origin, and finds that it also consists at first of cambium, so that each of the three tissues has its own peculiar cambium. These tissues are very often intermixed, and he terms such a mixture, which is produced from an effusion of the "*proxylaire*" cambium, into another already formed tissue, an "*adelome.*"—(*Link's Report*).

developed in bodies that originally consisted of nothing but cellular tissue; an embryo, for instance, is an aggregation of cells only; after its vital principle has been excited, and it has begun to grow, woody tissue and vessels are generated in abundance. We must, therefore, either admit that all forms of tissue are developed from the simple cell, and are consequently modifications of it; or we must suppose, what we have no right to assume, that plants have a power of spontaneously generating woody, vascular, and laticiferous tissue in the midst of the cellular. Mirbel has reduced the first of these suppositions to very nearly a demonstration; in a most admirable memoir on the development of Marchantia he speaks to the following effect:—"I at first found nothing but a mass of tissue composed of bladders filled with little green balls. Of these some grew into long slender tubes, pointed at each end, and unquestionably adhering by one of their ends to the inside of the sac; others from polygons passed to a spherical form in rounding off their angles. As they grew older, other very important changes took place in certain cells of the ordinary structure, which had not previously undergone any alteration: in each of these there appeared three or four rings placed parallel with each other, adhering to the membrane, from which they were distinguished by their opaqueness; these were altogether analogous to annular ducts. The cells become tubes did not at first differ from other cells in any thing except their form; their sides were uniform, thin, colourless, and transparent; but they soon began to thicken, to lose their transparency, and to be marked all round from end to end with two contiguous parallel streaks disposed spirally. They then enlarged, and their streaks became slits, which cut the sides of the tubes from end to end into two threads, whose circumvolutions separated into the resemblance of a gun-worm." In these cases there can, I think, be little doubt that the changes witnessed by Mirbel were chiefly owing to the development of a spiral thread in the inside of the tissue; he, however, did not consider it in that light.

The best general view of this subject is that of Schleiden, of which a full translation is published in the Annals of

Natural History, vol. vi. p. 36. He is of opinion that the cells of plants, including the so-called vessels, but excluding laticiferous tissue, allow of two periods being distinguished in their life.* In the first, which is that of their origin and isolated independent development, the membrane forming them grows, in its entire substance, by true intussusception. But as soon as the cells have adhered, to form the cellular tissue, and constitute the mass of a certain plant or its parts, this mode of growth either ceases entirely, or recedes so far into the background, that, from my observations up to the present time, I cannot venture to maintain its continuance; but neither can I deny it, because of the frequently very considerable expansion of the cells after the appearance of the succeeding formations. But in every case a new and very important momentum is added, by the deposit of a new layer on the inner surface of the cellular wall, and indeed everywhere, in the form of one or more spiral closely wound bands*, so that the coils, without continuity *inter se*, still mostly exhibit the completest contiguity. Hence proceed all the varied formations of cells and vascular walls according to the different influence of the following momenta:—

A. The most essential circumstance, and upon which is founded the division of all these textures into two large groups, that of *Spiroids*, and of *porous formations*, is the following: Either the cell has, at the time when the thickening of its wall by spiral deposition commences, already attained its complete expansion, or it has not.

1. Let us, in the first place, consider the latter case. Here, then, a second momentum becomes of importance; it is the cohesion both of the fibre and the cellular wall, and of the coils of the fibre *inter se;* at the same time, therefore, the number of fibres is likewise of value.

a. *Simple fibre.* The cell still expands considerably from the instant of its origin; some convolutions cohere early, others tear asunder: thus come annular vessels. In this case the fibre is generally not united at all with the cell membrane, or but loosely.

* Thus it appears that Schleiden supposes all the secondary layers of tissue to be spiral.

b. *Simple or compound fibre;* still a rather considerable expansion of the cell; slight, or no cohesion with the cell membrane: hence spiral vessels, with broad convolutions, capable of unrolling.

c. *Simple or compound fibre;* extremely slight expansion of the cell membrane, generally intimate cohesion with it; hence narrowly wound spiral vessels capable of unrolling, false tracheæ, and in part the ringed and scalariform vessels of older writers.

d. *Compound fibre;* moderate expansion of the cell, cohesion of the convolutions *inter se* in some places, generally also with the cell membrane. This produces the whole series of so-called branched and ramified reticulate spiral vessels. Hereto likewise belongs a portion of the striped and scalariform vessels of the older writers.

In these last, as well as in all the preceding, the law, that the more intimately the fibre coheres with the cell membrane, the less this can expand, appears to obtain.

2. But if the cell has, at the time when the spiral depositions have begun to form, already attained its complete expansion, a new and highly remarkable circumstance comes into action, namely, that the formation of air-vesicles on the outer wall of the cell, between it and the adjacent ones, precedes the origin of the deposits; and the convolutions forming, closely lying one upon another, and in most cases rapidly cohering *inter se*, separate from one another cleft-wise at the place which internally corresponds to those air-vesicles. Since this process can be followed very far, and yet cannot, on account of the minuteness of the parts, be observed in some formations otherwise exactly similar, sound analogy advises us to extend it to all porous textures. This slit, which is in general narrow, is often rounded by deposited matter which causes the pore to appear the rounder the more the cell is developed; the longer and more slit-like, the younger it is. To this division belong all porous cells and vessels, and likewise a portion of the young striped and scalariform vessels, which at that time only differ from those called pitted or porous by the length of the fissure.

B. A further advance consists in the progress of the cell

through various stages lying between the two extremes of the small and globular, and the much lengthened, together with an actual perforation of the primary membrane by absorption. To this head belong several formations, first indicated by Moldenhauer, and then correctly and fully described by Mohl, such as the leaf-cells of Sphagnum. But in this more especially consists the difference between cellular tissue and so-called vessels, the latter being nothing more than cylindrical cells, generally situated in the same direction, the terminations lying upon one another, their septa or partitions being perforated in a most varied manner by absorption.

C. Far more important, however, is the following circumstance:—In the vital process of cell-formation, spiral deposits are by no means at an end with the first layer; but they are repeated in many cases almost as frequently as the volume of the cell permits. The rule in such cases is, that the successive strata apply themselves exactly over and upon the first, so that the spaces of the cell-wall, not covered by the first deposit, likewise remain free from all succeeding deposits. Out of this arises the thickening of annular and spiral fibres to such a degree that they resemble plates, placed with their narrow edge on the cell-wall; as, for instance, in the species of Sphagnum, in the woody cells of Mammillarias, &c. The same class includes all those pitted cells, whose walls are thickened in a stratified manner. But anatomists are acquainted with some interesting exceptions to this rule. It sometimes happens that after the first spiral deposit has been altered by an expansion of the cell, a new layer is thrown down over the whole inner surface, whether fibre or primary cell membrane; and since this second layer stands in a different relation to the primary cell membrane from the first, it must also assume a different form, which is the porous. Such formations of distant fibres, between whose convolutions pores are found, are exhibited, in fact, by a number of dicotyledonous ligneous cells, especially in such plants as are subject to the powerful antagonism of the periods of vegetation and of winter sleep, as, for example, the Yew (*Taxus baccata*), the Linden (*Tilia europæa*), the Bird Cherry (*Cerasus*

Padus), &c. An analogous phenomenon is also found in the epidermis of the pericarp of Helleborus fœtidus.

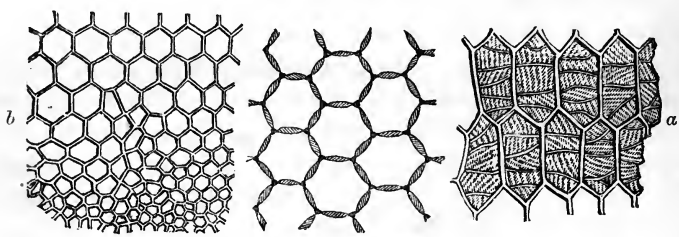
But although the origin of the different forms of tissue may be shown to be identical, it is obviously important to distinguish them for practical purposes, in order to avoid confusion, just as the organs of the flower, notwithstanding their common origin, are regarded as if they were essentially distinct. "If," as Link justly says, "we were to call the external parts of the flower of grasses, bracts, or leaves, because they, in point of fact, happen to be bracts, and eventually leaves, it would give rise to infinite confusion; and how many terms would not be necessary in order distinctly to express what bract or what leaf is alluded to? Raspail to be sure has adopted this singular manner of describing grasses, and no confusion has followed; but this is because nobody has given himself the trouble to introduce M. Raspail's treatise to notice." I shall therefore proceed henceforward to speak of them as if they were distinct in their origin.

SECT. I.—*Of Cellular Tissue, or Parenchym.*

CELLULAR, UTRICULAR, or VESICULAR TISSUE, generally consists of little bladders or vesicles of various figures, adhering together in masses. It is transparent, and in most cases colourless: when it appears otherwise, its colour is usually caused by matter contained within it.

If a thin slice of the pith of elder, or of any other plant, be examined with a microscope, it will be found to have a sort of honeycomb appearance, as if there were a number of

fig. 3.



hexagonal cavities, separated by partitions (*fig.* 3). These little cavities are the inside of bladders of cellular tissue; and the partitions seem to be caused by the cohesion of their sides, for if we boil the pith for a short time, the bladders separate from each other. In pulpy fruits, or in those which have their cellular tissue in a loose dry state when ripe, the bladders may even be separated from each other without boiling. It was formerly thought that cellular tissue might be compared to the air bubbles in a lather of soap and water; while by some it has been supposed to be formed by the doublings and foldings of a membrane in various directions. On both these suppositions, the partitions between the cells would be simple, and not composed of two membranes in a state of cohesion; but the facility with which, as has just been stated, the cellules may be separated, sufficiently disproves these opinions. But although the double nature of the partitions in cellular tissue may be often demonstrated, yet the cellules usually grow so firmly together, that their sides really form in their union but one membrane; and it will be hereafter seen that in many cases the partition between two cells is originally simple.

The cellular being regarded as the type of all other forms of tissue, the attention of anatomists has for a long time been directed to ascertaining in what manner it is originally produced. The nature of this inquiry is such, that great differences in opinion still continue to exist, as to a variety of points connected with it; and I do not think that we are yet in a condition to form any positive conclusion upon so difficult and obscure a point. The question is, however, one of so much interest that it seems desirable to explain at some length the views of the more experienced and sagacious of the observers who have devoted themselves to its investigation. In doing thus, I shall state the case in the form in which it stands in my "*Elements of Botany*," p. 10.

A. *Cells are produced by gaseous matter extricated among mucus.*—This is the idea which would strike all observers upon the examination of cellular tissue, with even the naked eye. We remember that it was formerly (about the year 1820), the opinion of Francis Bauer, and it is not yet certain

that the beginning of a cell may not be of this nature. Such a theory is not incompatible with the evidence revealed by the microscope as soon as the real structure of cells becomes visible; for there is a period anterior to the acquisition of such size as optical instruments can examine, in which we know nothing of what is taking place in the matter from which cells are derived. This is manifest upon the examination of cambium. It must, however, be a subject of hypothesis, because direct evidence upon the point is, from its nature, unattainable. It is no objection to this hypothesis that each cell has its own independent sides, because the same fact attends the extrication of gas in viscous fluids, and the intercellular matter may in that case be regarded as a remaining portion of mucus in which no gaseous matter has been formed.

B. *New cells are produced by old cells, on their outside, as new branches are produced by old ones.*—Amici says that the new tubes of Chara appear like young buds, from the points or axils of pre-existing tubes, an observation which has been confirmed by Slack. It has been stated by Mirbel that the same thing occurs in the case of Marchantia polymorpha. That learned botanist, in the course of his inquiries into the structure of this plant, found that in all cases one tube or utricle generated another externally, so that sometimes the membranes of newly-formed tissue had the appearance of knotted or branched cords. He satisfied himself that new parts are formed by the generative power of the first utricle, which spontaneously engenders on its surface others endowed with the same property. The amylaceous vesicles of malt in a state of fermentation manifestly produce new vesicles from their sides externally; and Turpin asserts that they also *contain* molecules, which are the rudiments of other cells.

C. *New cells are formed in consequence of the internal subdivision of an old cell by a plait, fold, or septum, projecting into its cavity.*—This, which is named "merismatic," or "fissiparous" development, is universal among pollen (which see hereafter), and has been regarded as the general mode of cell multiplication. The following observations by Mr. Thwaites upon certain Algals detail the appearances which lead to

this conclusion. They are, however, equally reconcilable with the next view (D.)

An Algal called Vesiculifera concatenata by Hassall, "occurs in ponds on a common near Bristol, and is of a pleasant pale apple-green colour. The cells are usually from five to seven times as long as broad, and are lined with but a small quantity of endochrome, which is disposed in a reticulate manner. Some of the cells, however, may be observed to be slightly inflated, and to contain a larger amount of endochrome than the rest; in each of these inflated cells a spore is subsequently formed, and in the following way:—The endochrome, after attaining a certain degree of density from an increase in its development, not from any derived from a contiguous cell, moves towards one end of its cell; it (the endochrome) shortly becomes divided into two very unequal portions, the larger and terminal one of which becomes converted into the spore, and the smaller portion is found to be separated from this by a single septum. A process has, in reality, taken place analogous to the fissiparous division of the cell of Zygnema; two cells have been formed within the original one, but in the Vesiculifera one of these new cells is the spore.—In V. æqualis, I have been able to trace the mode of development of the two or three contiguous spores, which are sometimes to be seen in the filaments of this species: the first spore is formed in the way I have previously mentioned, and arrives at considerable maturity before there is any appearance of one, contiguous to it, being produced; but it may then be seen that the smaller portion of endochrome, which had been separated just previously to the first spore being formed, and which then occupied but little space in the cell, has become considerably increased in amount. An increase having also taken place in the length of the cell: at length the process of division, &c., occurs as before, and a second spore is formed adjoining the first. The formation of a third spore involves a similar chain of phenomena." (*Annals of Natural History*, vol. xvii. p. 334.)

D. *Cells are produced by a stricture of the sides of an original cell, which stricture eventually divides the latter into two cavities.*—This view is supported by the evidence adduced by

Mohl. From the observations of this anatomist it appears that in Confervæ the increase in number of the cells takes place by the internal division of a parent cell. In Conferva glomerata the last joint is always as long as those below it, only rather more slender. The branches grow at the upper lateral extremity of a joint or cell; each at first is a small protuberance, which is transformed into a lateral cylindrical excrescence containing chlorophyll (green colouring matter), and having its cavity in communication with that of the joint which bears it; as the branch lengthens, a contraction is observable at the line of insertion, which contraction is directed towards the interior of the cell, and chokes up the green matter, forming a sort of partition, pierced in the middle like a ring. This partition grows with the growth of the branch, and at last completely cuts off all communication between the first cell and its branch. Thus cut off, the latter lengthens by degrees, till it forms a very long cylindrical cell, which divides in just the same manner into two other cells, the terminal of which alone lengthens, to be bisected in its turn.

Mr. Henfrey, in an able paper read before the British Association, Sept. 1846, produces new evidence in support of this opinion, viz.:—"That the division of a parent cell into new cells is effected by the gradual folding inward of the primordial utricle, which organ, in virtue of its peculiar function, secretes the septum within that fold; the circular constriction thus produced arriving finally at the centre, the septum consisting of a double layer of cell-membrane becomes complete." The evidence upon which he relies is stated thus:—"In the course of my investigations to satisfy myself of the correctness of the view I had taken of the agency exercised by the primordial utricle in cell-division, I have observed the process in several plants, Cryptogamous and Phanerogamous. In no case have I been able to trace the gradual progress of the formation of septa so well as in Achimenes grandiflora. This plant produces a great number of axillary buds or bulbets, on the scales of which are found many capitate hairs. I examined these hairs in young buds of from about half a line to a line in length, possessing at that period only six or seven scales. By dissection these

scales were isolated and brought under the microscope; the hairs which fringed the margin of the scales were thus presented free throughout their whole length, and being very transparent, afforded an admirable opportunity of examining the cells in their different stages in a perfect and uninjured condition, an important point which cannot be secured in sections of growing tissues. In the earliest stage the nuclei were perfect and distinct one from another; in the next, the transverse lines indicate the commencement of the infolding of the primordial utricle; that the lines are not septa is seen by the appearance of hairs which had been kept in spirit several days; in these, the primordial utricle, detached from the lateral walls, is continuous throughout the whole length of the hair. Different stages of the infolding, that is, the progress of the fold towards the centre, are shown by the constrictions exhibited by the coloured mucilaginous cell-contents. In a specimen treated with iodine, the septa were incomplete in the upper part of the hair, but the lowest septum was perfect—the primordial utricle with the cell-contents having become retracted from it. In this septum two new layers may be traced from the lateral walls, intimately united toward the centre, so as to appear like one layer. This example also showed that the layers forming the septum are continuous with a new layer deposited over the inside of the lateral wall. Mohl states that each layer of new matter grows from the circumference to the centre, and that the septum is not produced by a succession of layers; each projecting a little beyond that preceding it. This point I have not yet been able to determine for myself. In the perfect cell, the primordial utricle, with the nucleus, undergoes dissolution." (*Annals of Natural History*, vol. xviii. p. 367.) "These views, however," adds Mr. Henfrey, "which I have adopted of the nature of the process of multiplication by division, are not sufficient to explain all cases of cell-development,—I allude particularly to the production of free cells in the cavity of a parent cell, such as occurs in the formation of spores and pollen. Supposing that this is not effected in the way described by Schleiden, namely, by development from nuclei, it is necessary to suppose, either with Nägeli, that the

primordial utricle divides into distinct portions and becomes detached from the cell-wall before it begins to secrete membrane, or that the new cells formed within the parent-cell, subsequently become free by the solution of those layers of membrane deposited immediately upon the primary walls." (*Ibid,* where there is an excellent set of figures.)

E. *There is produced among mucus a* Cytoblast, nucleus, *or* central point, *which acts chemically upon the matter in contact with it, until it forms a firm layer. This layer is a closed bladder, or vesicle, which enlarges by assimilating the fluid, and becomes a cell, to whose inside wall the Cytoblast, which does not grow to the same extent, remains attached, in the form of a circular space or disk.*—This theory, which may be regarded as an attempt at explaining original cell formation, rather than the later forms of cell multiplication, originated with Schleiden, who first knew how to apply a curious discovery made by Francis Bauer.

In the centre of some of the bladders of the cellular tissue of many plants there is a roundish body, apparently consisting of granular matter, the nature of which is unknown. It was originally remarked by Francis Bauer, in the vesicles of the stigma of Phaius Tankervilliæ. A few other vegetable anatomists subsequently noticed its existence; and Brown, in his Memoir on the mode of impregnation in Orchids and Asclepiads, has made it the subject of more extended observation. According to this botanist, such nuclei not only occasionally appear on the epidermis of some plants (Plate III. fig. 9.), in the pubescence of Cypripedium and others, and in the internal tissue of the leaves, but also in the cells of the ovule before impregnation. It would seem that Brown considers stomates to be formed by the juxtaposition of two of these bodies, which he calls *nuclei,* a term that usually belongs to the ovule. (See also Slack, in the *Trans. Soc. Arts,* xlix.) Schleiden has published some extremely interesting observations upon this body, which he regards as a universal elementary organ, and calls a *Cytoblast.* According to him, the *form* varies from oval to lenticular and round, the *colour* from yellowish to a silvery white, changing to pale yellow up to darkest brown upon the application of iodine: in *size* it

varies between $\frac{1}{2200}$ of a Paris inch in diameter, in Fritillaria pyrenaica, where it attains its largest size, and $\frac{1}{10000}$ in the embryonal end of the pollen tube of Linum pallescens. In *structure* it is usually granular; in *consistence* it varies between extreme softness and such a degree of toughness, as enables it to resist the action of a Compressorium without altering its form. In the interior of the Cytoblast, or sunk in its surface, is a small, well-defined body, which, to judge from its shadow, represents a thick ring or a thick-sided hollow spherule: there is generally but one such spherule to each Cytoblast, but occasionally there are two or even three. The spherule varies in size from half the diameter of the Cytoblast to a point too small to be measured; and Schleiden believes that this minute body is formed earlier than the Cytoblast itself. It is sometimes darker, sometimes clearer than the rest of the Cytoblast; and is usually of a firmer consistence, remaining well defined when the latter is crushed by pressure into amorphous mucus. If the gum which is found in the youngest albumen of a plant be examined, it will be found turbid with molecules of extreme minuteness. Of these some acquire a larger size and a more definite outline than others, and by degrees Cytoblasts appear, which seem to be a granular coagulation round each molecule. As soon as the Cytoblast has attained its full size, there appears upon it a fine transparent vesicle; this is a young cell, which at first represents a very flat segment of a sphere whose flat side is formed of the Cytoblast and convex side of the young vesicle. The space lying between the convexity of the vesicle and the Cytoblast is as clear and transparent as water, and is apparently filled with an aqueous fluid. If these young cells are isolated, we may, by shaking the field of the microscope, wash the mucous molecules almost clean; but they cannot be long observed, because they dissolve in distilled water in a few minutes, and leave nothing but the Cytoblast behind. The vesicles continue to swell out, and their lining becomes formed of jelly, with the exception of the Cytoblast, which soon becomes a part of their wall: the cell keeps increasing in size, till at last the Cytoblast forms a new wall on the free side, and so becomes imbedded in the side of the cell, or it

remains loose in the cavity. It is, however, in time absorbed, and it is only after its absorption has occurred that, as Schleiden believes, the process of depositing secondary layers begins. The Cytoblast appears, however, sometimes to have a permanent existence, as in the pollen of Larix europæa, and in those hairs in which a circulation of the sap is observable; in them Schleiden has remarked (and the observations of myself and others coincide with his), that all the currents proceed from the Cytoblast, and return to it as to a common centre. Mr. Henfrey objects to this theory upon the ground that two cells may be formed by the division of a parent cell, *without any change in the position of the contents.* This he regards with much reason as a decided proof that the two new cells did not originate free, of small size, and afterwards grow to fill the parent cell, because in that case the original contents of the parent cell *must have been outside the new cells,* and therefore, in order to be found in the interior of the latter, must necessarily have been dissolved, absorbed, and re-deposited, which has not been seen to happen.

F.—*Cells proceed from* nucleal vesicles (*Cytoblasts*), *inclosing dense mucilage, with one* nucleolus *or more. These nucleoli are probably also vesicles of a mixed order, filled with mucilage. The nucleal vesicles, which may be either free or attached to the wall of a cell, send out many thread-like currents of sap into the cavity of the cell, and thus become foci of vitality, by whose action the walls of the cell are formed and nourished.*— This theory, which in many respects is like that of Schleiden, has been proposed by Carl Nägeli, whose elaborate and admirable memoir on cell formation has been well translated for the Ray Society by Mr. Henfrey. The following extract will assist the reader in understanding his peculiar views:—

"Cell-nuclei (Cytoblasts) occur in all classes and orders of plants. The number of plants in which they have not yet been found, is comparatively very small. The exception in these cases may justly be attributed to insufficiency of observation, on account partly of the minute size of the nascent cells (in Lichens, many fungi), partly of the extraordinary size of the cells (Siphoneæ), and partly of the opacity of the contents of the young cells (some Confervæ and Siphoneæ.)

In no vegetable cells has it yet been, or probably ever will be, demonstrated, that the nucleus is absolutely wanting. On the contrary, wherever observation has been possible, it has enabled us to recognize one. If, therefore, it is ever permissible to draw a conclusion from analogy, it must be so here, and lead to the decision that the nucleus is an universal and unexceptional phenomenon in vegetable cells. This assumption is so much the more justifiable since it does not merely conclude from nine-tenths as to the remaining tenth, but altogether from like to like. For there is no special kind of cell, in which an example of the nucleus has not already been demonstrated, while, in regard to all cells where it has not yet been seen, individuals of the same kind are known which possess it.

"Cell-nuclei are primary or secondary, according to the epoch of their origination. They have a perfectly distinct relation to the vital process of the cell. The primary nuclei precede the cell; they make their appearance first in the parent cell, and determine the formation of the progeny cells. They exhibit two kinds of relation of position. That of the first is where the primary nucleus lies free, and more or less in the centre of the cell, which has been produced by its influence. This is the case in the vegetative cells of all true Fucoids and some green Algæ (Conferva bombycina, Spirogyra, Closterium, &c.), and in the special parent cells of all plants which produce four spores or pollen grains in one parent cell. (Florideæ, Hepaticæ, Musci, Filices, Lycopodiaceæ, and Phanerogamia). The secondary kind of primary nuclei are attached upon the wall of the cell which they produced. Such nuclei are possessed by all cells (with the exception of the special parent cells) of those plants which produce four spores in a parent cell (Phanerogamia, Lycopodiaceæ, Filices, Musci, Hepaticæ, and Florideæ); also the cells of Equisetaceæ and Characeæ; lastly, the cells of some Algæ (Arthrodesmus, Gaillionella, Bangia), and numerous Fungi.

"The secondary nuclei make their appearance in the cell at a later period; they do not serve to produce new cells, but are, apparently, at once the expression of an exalted vital

activity of the cell, and the support of it. They lie free in the cavity of the cell, single or in large numbers, and appear with the primary nucleus, or not till after its absorption. The presence of secondary nuclei has only been determined, as yet, in cells with a parietal primary nucleus, not in such as have a free primary nucleus. Their presence is as yet restricted to the pollen cells and the pollen tube, to the spores and the embryo-sac, to the parent cells of pollen grains, and those spores which originate in fours.

"Where the nuclei were large enough to allow of an accurate microscopical examination, the following structure was perceived:—the nucleal vesicle consists of a peculiar membrane, and incloses fluid and solid contents distinct from it, and, in addition to one or more dense mucilage corpuscules, a nucleolus. That the nuclei possess a membrane, and therefore are utricles, follows from the correspondence of the results of researches in Algæ, Fungi, Florideæ, Hepaticæ, Musci, Filices, Characeæ, Equisetaceæ, Lycopodiaceæ, and Phanerogamia. This structure is demonstrated both in the free and the parietal nuclei. Where the membrane cannot be seen, it is on account of the minute size of the nucleus, of its being densely filled with homogeneous substance, or of the opacity of the cell-contents. In larger nuclei, where a more certain examination is practicable, the absence of the membrane can never be demonstrated. Even where the membrane is overlooked in the natural condition, on account of the similarity of the contained matter, it may be made visible by the action of re-agents. (Filices.) There is no reason, therefore, against stating, as a general proposition, that the nuclei are utricles.

"The nucleus is not merely universally an utricle; it also possesses a proper membrane, and a peculiar metamorphosis of its contents. It cannot be demonstrated by direct examination, that the membrane is not merely a deposit (distinct from the nucleus) from the surrounding fluids of the cell. That it constitutes in its totality a distinct organ, is shown by the power of the nucleus to propagate as an utricle. I have pointed out the division of the nucleal vesicle in the Hepaticæ (Anthoceros,) and in the Phanerogamia (Trades-

cantia.) The contents of the nucleal vesicle run through a series of alterations. These consist, morphologically, in this: from the amorphous mucilage, granules are formed, which lie in a watery fluid; chemically, in this: from a mixture of mucilage and gum are produced mucilage, starch, and chlorophyll-granules, oil-globules, and colouring matter. The vital processes, the fashioning, (Gestaltung), and the propagation of the nucleal vesicle, agree in general with those of the cell, and it must in like manner be regarded as an individual organism.

"The nucleus, when fully developed, contains one or more nucleoli. This structure I have pointed out in free and parietal nuclei in the Algæ, Fungi, Florideæ, Hepaticæ, Musci, Characeæ, Equisetaceæ, Filices, Lycopodiaceæ, and Phanerogamia. In many nuclei, however, the nucleolus has not yet been detected. This is most striking in the Fucoideæ, where the nuclei are quite large, and can readily be set free. The investigation is rendered very difficult in these by the peculiarity of the cell-contents. Moreover, the nucleal vesicles are for a long time densely filled with mucilage, and in a condition that, even in the Phanerogamia, usually renders the observation of the nucleoli impossible. All other nuclei without nucleoli (and to these belong only the nuclei of several Fungi and most Algæ) are small, or the opacity of the cell-contents renders an accurate examination impracticable. At this time I know of no nucleus in which the absence of the nucleolus has been distinctly made out; I am inclined, therefore, to set forth generally, and to claim as an essential character of the nucleal vesicle, that it contains one or more nucleoli. Although the old and metamorphosed nuclei in Cystoseira, which sometimes possess merely a membrane with transparent contents, certainly no longer contain nucleoli, this does not argue against the assumption; since in old cells, in which the chemical changes of the contents are completed, the nucleus also is mostly absorbed.

"The assumption that the nucleus has the complex structure above indicated, might indeed be an improbable one as to the small point-like nuclei of those cellules, in which the

motile spiral threads, spermatic filaments, are formed in Florideæ, Hepaticæ, Musci, Characeæ, and Filices. I believe, however, that the cellules in that case have not the signification of cells, but of nucleal vesicles, and therefore that the nucleiform body is not a nucleus, but a nucleolus. This assumption is perfectly natural in the Characeæ, as there the cellules of the spermatic filaments are to be distinguished as special structures inside the actual cells. In other Cryptogamia, which possess the so-called spermatic animalcules, experience can offer proof neither for nor against, as at present we are altogether without facts as to the history of their development.

"As to the structure of the nucleoli, in my opinion nothing universal or precise can as yet be said. In some cases they appear to be merely accumulations of mucilage. In others, a membrane which surrounds them is wholly unmistakeable. In every case it is certain that they always appear with a clearly defined margin. This circumstance speaks strongly in favour of the assumption that they, like the nuclei, are inclosed in an utricle. Since, if they were merely agglomerated mucilage, we should have nucleoli, the substance of which would pass gradually into the mucilage of the nucleal vesicle, and which would generally possess an irregular periphery. Or if they originated by the deposition of layers from without, this lamellar structure would be perceptible in large and perfect nucleoli. Not only is there nothing of the kind to be seen, but the facts of the appearance of hollow space, the whole mass becoming vesicular, and the change into a granular substance, testify against it. The presence of a membrane is now indeed indubitable in some nucleoli. It is, however, still a question whether this is not somewhat accidental, whether it does not represent merely the thickened outermost layer of mucilage; since also where a hollow space makes its appearance in the contents of the nucleal vesicle, around the nucleolus, this becomes hardened into a membranous structure on its bounding surface. So long, too, as the membrane of the nucleolus, from its vital history, does not appear to be anything essential (as that, for instance, in the nucleal vesicles resulting from propagation), I cannot, from its presence in individual

cases, deduce a safe analogy applicable to all." (*Ray Reports*, 1846.)

G. *Cells are formed by Cytoblasts generated amidst mucus or protoplasm, by the action of the Cytoblast and certain electrical currents connected with it, of which forces the Cytoblast is the centre. The electrical currents are caused by chemical changes, arising from the vital processes, which go on amidst the endochrome or contents of the cell.*—In this point of view the cell-membrane is regarded as of no further importance to the cell-contents or endochrome than as an external guard to them; the vital processes and the production of the membrane itself being carried on by their contents, in which alone vitality resides. "If," says Mr. Thwaites, "a decaying vegetable organism is brought before us, in which nothing remains of the former structure but the cell-walls, it is difficult to conceive that this skeleton, as it were, has performed an important part in the vital processes of the plant, that it has been an important agent in the chemical changes which had been going on during the processes of secretion, assimilation, &c.—in fact, that it has been any other than a mere skeleton for the support of the important parts of the organism"—a shell as it were to protect them. This remarkable theory is of so much importance that, in justice to its author, his views must be given as nearly as possible in his own words. The original, with all the details which I have been obliged to omit, will be found in the *Annals of Natural History*, vol. xviii. p. 15.

"There cannot be a more satisfactory way of showing the subordinate character of the cell-membrane than by exhibiting a perfect living organism in which it does not exist, and there are some plants, belonging to the family Oscillatoricae, in one of which (a species of Spirulina) there appears to be no real membrane—the plant consisting of a mucous matrix, out of which, when the species is mature, emerge oscillating spiral filaments, which from their exhibiting no trace of cell-membrane, or even of any division, by septa, into separate portions, and from the rapidity with which they become decomposed, I believe to be continuous masses of endochrome held together by mucus. Another species to which I would direct attention

is the Lyngbya ferruginea, Agardh, a plant scarcely differing from Oscillatoria, except in the greater firmness of the membranous sheath which invests each filament: the filaments of this plant are composed of lenticular masses of endochrome and during the early part of their growth are inclosed in a membranous sheath; from this, however, they emerge when mature, and soon afterwards become broken up into the separate masses of endochrome, each of which appears to be held together by a kind of mucus, and not to be surrounded by a cell membrane.

"I now proceed to point out instances in which the cell-membrane is seen to be of quite a secondary character; and that its development is regulated entirely by the condition of the endochrome it contains, and that, in fact, it owes its existence to this endochrome. The production of cell-membrane and endochrome has the appearance frequently of being synchronous, but the endochrome may sometimes be seen becoming invested with a cell-membrane, and this may be well observed during the formation of the spore of Zygnema and other species of Conjugatæ. Those who have paid attention to this family of plants are well aware, that previously to the formation of the fruit, two cells unite by means of a short tube developed from each, and through the canal formed by the union of these the endochrome of one of the cells passes into the other cell, becomes mixed with its endochrome, and subsequently around this mixed endochrome a cell-membrane is developed. This membrane would certainly appear to be developed by the endochrome and not by one of the original cell-walls, otherwise we could not expect it to be entirely influenced as to its form and size by the contained endochrome, but that there would be indications of its being independent of this. The spore-membrane, however, not only corresponds in extent with the contained endochrome, but if, as is sometimes accidentally the case, the mass of endochrome has become divided into two portions, each of these portions becomes covered with a cell-membrane; thus showing that the relation is between these and not between either and the original cell-wall.

"An abnormal growth which sometimes takes place in the

cells or long tubes of Vaucheria will serve well to illustrate how immediately an increased production of cell-membrane is consequent upon an additional development of endochrome. The cells of Vaucheria are occasionally found to be infested with a species of Vorticella, an infusory animalcule. This little animal is seen occupying large pear-shaped protuberances upon the frond of Vaucheria, in which it deposits its ova. Now it is interesting to observe the mode in which these peculiar protuberances are formed. The Vorticella may, in some instances, be seen within the tube of the plant, and from the slight alteration in the endochrome, it may be inferred that the little animal has not been long present there; in other cases it may be observed that the presence of the Vorticella has caused an evident dilatation of the cylinder of endochrome with a corresponding enlargement of the cell-membrane; whilst in other examples this dilatation has gone on so as to have produced a large pear-shaped appendage to the frond, within which the Vorticella may be seen moving. But what I would wish particularly to draw attention to, is the fact that the stimulus arising from the presence of the Vorticella has been operating immediately upon the internal surface of the cylinder of endochrome, causing an abnormal development of this, accompanying and consequent upon which has been a corresponding and regular development of cell-membrane; showing that the amount of production of cell-membrane is regulated by the growth of the endochrome."

The author then proceeds to remark "upon a structure which is developed in greater or less amount in most Algæ,—external to the cell-membrane,—possessing some characters in common with it, and probably in many cases performing a similar office in the economy of the organism. The structure I allude to is the mucus which surrounds the cells of Algæ, and in some species, such as in many of the Palmelleæ, of considerable extent, so as to make up by far the greater part of the plant. In some of the Palmelleæ indeed, the plant at first sight appears to be composed of an amorphous gelatinous mass, containing cells imbedded in it, and would lead to the idea that this gelatinous mass is the matrix from which the cells are developed, and to which they owe their origin; but

such is really not the fact. There are some species of Palmelleæ which show the character of this mucus very clearly, and in which its development can be traced without difficulty."

"In Coccochloris cystifera may be readily observed the circumstances under which the mucus is developed, and that this mucus is of definite form and quantity. This, like most if not all Palmelleæ, increases not only by an enlargement of its cells, and the ordinary reproduction of these from a parent cell or spore, but during the development of the plant the number of cells is much increased by fissiparous division, each cell becoming divided into two or four, no doubt in the same way as occurs in Zygnema, Isthmia, &c. Now if the plant in which this process is going on be carefully examined, it will be seen that the mucus is developed in definite quantity around each cell, and doubtless by it. For we may perceive one cell in which there is no indication of fissiparous division; another in which this process has just taken place, but the cells are yet in close opposition; another in which the two new cells are separated to some distance from each other; and if we examine into what has led to their separation, we may find that this arises from a definite development of mucus around each of them, and within the mucous envelope of the original cell; and lastly, we may find a pair of new cells of nearly equal size with the original one, each with nearly the ordinary amount of gelatine or mucus surrounding it, and the mucous sheath of the original cell nearly absorbed. In a Palmella found in Sussex by Mr. Jenner, and sent me by Mr. Ralfs under the name of P. hyalina, the original mucous sheath appears not to be absorbed, but to be ruptured upon the production of new ones within it. Each cell of some species of this family is surrounded by two or more distinct mucous envelopes; and in some species a cluster of cells is also surrounded by a common mucous sheath, which is no doubt also developed from the cells. The curved moniliform filaments of the genus Nostoc would at first sight appear to grow in a mass of gelatine without any definite arrangement; but when, as is sometimes the case, the plant occurs with a single straight filament, this is found to be surrounded by a

gelatine or mucus of definite diameter, showing that in this genus the amount of gelatine depends upon the number of cells. In a freshwater species of Schizonema, occurring abundantly in the neighbourhood of Bristol, the common mucous sheath is liable to considerable modification according to the circumstances under which the plant grows. It occurs in some situations in the form of a mucous stratum upon the surface of stone; in others the gelatinous sheath is of extreme tenuity and transparency: whereas, if the plant is found in rather deep rapid streams, the sheath is much developed, and becomes of almost membranous texture; thus showing that this gelatinous structure is of subordinate character, and may vary according to the circumstance in which the plant is found." If these statements are true of Algals, the same explanation would apply to higher plants; and Mr. Thwaites regards it as not improbable, that the deposits of sclerogen as well as the firm portion of the spiral fibre may be considered as structures of a similar character. "The pellicle which covers the epidermis is doubtless so. Now what is the character of the mucus which we have seen to be developed in definite quantity outside and around the cell-wall? That it is not a mere chemical solution of starch would appear evident from its persistence when mounted for the microscope in water and other fluids. Its toughness and elasticity, the readiness with which it allows water to permeate it, and its recovering its original form and consistence upon being moistened after desiccation, seem to warrant the belief that it possesses an organised form of the same mechanical properties as sponge.

"As, in viewing a series of Algæ, a transition may be observed from a mucous structure to one possessing the external characters if not the functions of cell-membrane; it may be inferred that cell-membrane is of a similar mechanical structure, and we should perhaps not be far from a right definition in applying to it the term felt, as indicating its real characters." These are the considerations that have led Mr. Thwaites to the conviction "*that cell-membrane is quite a subordinate part of living structure; that its functions are of a purely physical character; that its principal office is to*

protect, locate or isolate, the matter it contains, and that any vitality it possesses is derived from the presence within it of its endochrome. There are, however," he proceeds, "a few phenomena which at first sight would appear to militate against the opinion I have advanced; I mean the contractility of certain membranes and the movement of ciliary appendages belonging to others. It is very certain, that during the vital processes which are going on in the interior of the cell, considerable chemical changes take place; and these must of necessity give rise to an elimination of electrical currents. The presence of such currents would, I think, be sufficient to account for the rhythmical movement of ciliæ, as well as for the contraction of membranes of certain mechanical structure.

"I would ask whether these electrical currents may not give rise to the formation of the mucus surrounding the cell, and determine its character and extent; whether, too, the production of cell-membrane may not occur under a similar influence; and whether this would not be the easiest solution of the problem of how the cell is increased in size? viz. that a formation of cell-membrane takes place within the range of these currents, whilst absorption occurs within or without it. On this principle, too, we can better understand the process of the fissiparous division of cells; the endochrome becoming divided into two portions, two centres of electrical force are originated, and each of these giving rise to a set of currents, two cell-membranes are produced instead of the original one. The frequent occurrence of nests of regular crystals (not sand) in the substance of the mucous envelopes of such freshwater genera as Batrachospermum, Chætophora, and Monormia, would seem to afford positive proof that electrical currents exist there.

"These views, if correct, would, of course, apply to animal as well as vegetable organisms, and we should be under the necessity of considering the entire membranous or solid portion of the animal as of a subordinate character to the fluids contained in its cells, and merely as an instrument acting in prompt obedience and conformity to the changes taking place in these fluids.

"But treating the subject of the functions of the cell-membrane in a chemical point of view, we know that considerable chemical changes are taking place during the processes of assimilation, secretion, elaboration, &c., and that these are essentially chemical phenomena. Are we to look to an organ of such a low chemical constitution as cell-membrane as likely to give origin to the initiative in these important changes? I cannot believe such can be the fact, but that the organ or substance which gives a start, as it were, to these phenomena, will be found to be one in which rapid chemical change is taking place—one which, under the influence of light, &c., acting upon substances brought into contact with it, brings about a change in these; these changes again reacting upon itself. I cannot help believing that such will prove to be the explanation of the various phenomena of animal and vegetable growth. On a chemical difference in the constitution of this primary organ,—a difference not likely ever to be appreciable by chemists, any more than microscopists will ever be able to discern the ultimate atoms of bodies,—may possibly depend the endless variety of forms put on by organic nature. From a germ of great external similarity they all alike originate; but that these germs are not really alike is shown by their subsequent behaviour. They have different properties: does not this imply a different constitution? a different chemical constitution?"

This theory of Mr. Thwaites has lately received fresh support from an observation by Dr. Dickie, of Aberdeen, (*Notes on Algæ*, p. 10), that the cells of Hæmatococcus binalis, a beautiful Brittlewort (Diatomacea), have, when fresh, *a power* of rotation in the interior of the mucous matter which surrounds them; a phenomenon which Dr. Dickie compares to the revolution of the yolk in the ova of certain Mollusks, as was observed long ago by Leuwenhoek.

The bladders of cellular tissue are destitute of all perforation or visible pores, so that each is completely closed up from its neighbour, as far as we can see; although as they have the power of filtering fluids with rapidity, it is certain that they must abound in invisible pores, and that they are not

impermeable, as if they were made of glass. Probably the suggestion of Mr. Thwaites (page 43), that their sides should be regarded as being spongy, is a near approximation to the truth. An opinion different from this has been entertained by some observers, who have described and figured perforations of the membrane in various plants. Mirbel formerly stated that "the sides of the bladders are sometimes riddled full of holes (*fig.* 4), the aperture of which does not exceed the $\frac{1}{300}$ of a millimetre (or of half a line); or are less frequently pierced with transverse slits, which are occasionally so numerous as to transform the bladders into a real articulated tissue, as in the pith of the Nelumbium (*fig.* 5)." This statement is now well known to have been founded upon inaccurate observation; what the supposed pores really are has already been explained. (See page 18).

fig. 4.

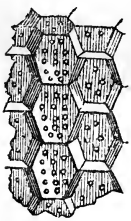


fig. 5.

The only case of undoubtedly perforated parenchym with which I am acquainted is in Sphagnum, where it was first noticed by Mr. Valentine (*Muscologia Nottinghamiensis,* No. 1. 1833). He correctly describes this genus as having the exterior cells of its branches furnished with an aperture communicating with the external air. "The aperture is tolerably distinct in S. acutifolium; it is situated at the upper end of the cell, and stands off obliquely, appearing like a minute truncated cone. An easy way to observe it is, to press out the air contained in the cells, which escapes from the aperture in a minute bubble." This curious contrivance might have been supposed analogous to the air passages into the trunk, below the insertion of the leaves of Tree Ferns, if it did not equally exist in all the parenchym of the leaves themselves. Mr. Valentine does not notice the latter fact, and I believe he considers the circles in the leaves of Sphagnum not to be apertures: but I had ascertained, by Mr. Reade's ingenious charring process, that they undoubtedly are openings, before I saw John Röper's paper upon the subject in the *Annales des Sciences* (n. s. x. 314). This writer proved that the circular spaces in Sphagnum leaves are openings, by observing the exit and entrance

through them of the Rotifer vulgaris, and of minute granular matter. He considers the openings intended "to guarantee the organs of respiration from the too great influence of the air." But I do not perceive in what way such an effect is to be accomplished. Similar openings are found at the point of contact of the ends of spiral, and other vessels, or tubes.

With reference to this subject, it may be observed, that the bladders of cellular tissue often contain air-bubbles, which appear to have no direct means of escape, and that the limits of colour are always very accurately defined in petals, as, for instance, in the stripes of tulips and carnations, which could not be the case if cellular tissue were perforated by such holes as have been described; for in that case colours would necessarily run together.

Cellular tissue is generally transparent and colourless, or at most only slightly tinged with green. (See page 10). The brilliant colours of vegetable matter—the white, blue, yellow, and scarlet hues of the corolla, and the green of the bark and leaves—is not owing to any difference in the colour of the cells themselves, but to colouring matter of different kinds which they contain. In the stem of the Garden Balsam (Impatiens Balsamina), a single cell is frequently red in the midst of others that are colourless. Examine the red bladder, and you will find it filled with a colouring matter of which the rest are destitute. The bright satiny appearance of many richly coloured flowers depends upon the colourless quality of the tissue. Thus, in Thysanotus fascicularis, the flowers of which are of a deep brilliant violet, with a remarkable satiny lustre, that appearance will be found to arise from each particular cell containing a single drop of coloured fluid, which gleams through the white shining membrane of the tissue, and produces the flickering lustre that is perceived. [The cause of colour in plants will be spoken of hereafter in the second book.]

The bladders of cellular tissue develope, in some cases, with great rapidity. I have seen Lupinus polyphyllus grow in length at the rate of an inch and a half a day. The leaf of Urania speciosa has been found by Mulder to lengthen at the rate of from one and a half to three and a half lines per hour,

and even as much as from four to five inches per day. But the most remarkable instances of this sort are to be found in the mushroom tribe, which in all cases develope with surprising rapidity. It is stated by Junghuns, that he has known the Bovista giganteum, in damp warm weather, grow in a single night from the size of a mere point to that of a huge gourd. We are not further informed of the dimensions of this specimen; but supposing its cellules to be not less than the $\frac{1}{200}$ of an inch in diameter, and it is probable they are nearer the $\frac{1}{400}$, it may be estimated to have consisted, when full grown, of about 47,000,000,000 cellules; so that, supposing it to have gained its size in the course of twelve hours, its cells must have developed at the rate of near 4,000,000,000 per hour, or of more than sixty-six millions in a minute. This can be compared to nothing except the effect of liberating gas among mucus, and seems to be irreconcilable with any other kind of development (see page 27), unless it is assumed that in such cases cells are originally in a state of violent compression, from which they spring up when the pressure is removed.

Cellular tissue grows for a long time after its generation, and hence the bulk of a given part may be much increased without the addition of any new elementary organs. Link states that in the branch of a Pelargonium cucullatum, about 1 line in diameter, he found the larger cells $\frac{1}{21}$ of a line broad, while in an older branch of the same plant, 2 lines in diameter, the larger cells were $\frac{1}{10}$ of a line broad; hence it was evident that the growth of the branch depended upon the growth of the individual cells.

The bladders of cellular tissue are always very small, but are exceedingly variable in size. The largest are generally found among Cucurbits, or in pith, or in aquatic plants; and of these some are as much as the $\frac{1}{50}$ of an inch in diameter; the ordinary size is about the $\frac{1}{400}$ or the $\frac{1}{500}$, and they are sometimes not more than the $\frac{1}{1000}$. Kieser has computed that in the garden pink more than 5100 are contained in half a cubic line.

Cellular tissue is found in two essentially different states, the *membranous* and the *fibrous*.

Membranous Cellular Tissue is that in which the sides consist of membrane only, without any trace of fibre; it is the most common, and was, till lately, supposed to be the only kind that exists. This sort of tissue is to be considered the basis of vegetable structure, and the only form indispensable to a plant. Many plants consist of nothing else; and in no case is it ever absent. It constitutes the whole of Mosses, Algals, and Lichens; it forms all the pulpy parts, the parenchym of leaves, the pith, medullary rays, and principal part of the bark in the stem of Exogens, the soft substance of the stem of Endogens, the delicate membranes of flowers and their appendages, and both the hard and soft parts of fruits and seeds.

It appears that the spheroid is the figure which should be considered normal or typical in this kind of tissue; for that is the form in which bladders are always found when they are generated separately, without exercising any pressure upon each other; as, for example, is visible in the leaf of the white lily, and in the pulp of the strawberry or of other soft fruits, or in the dry berry of the Jujube. All other forms are considered to be caused by the compression or extension of such spheroids, or by the action of organisable matter in unequal degree.

When a mass of spheroidal bladders is pressed together equally in all directions, rhomboidal dodecahedrons are produced, which, if cut across, exhibit the appearance of hexagons. (Plate I. fig. 12.) This is the state in which the tissue is found in the pith of all plants; and the rice paper, sold in the shops for making artificial flowers, and for drawing upon, which is really the pith of a Chinese plant, is an excellent illustration of it. If the force of extension, or compression, or nutrition, be greater in one direction than another, a variety of forms is produced, of which the following are the most worth noticing:—

1. The *oblong;* in the stem of Orchis latifolia, and in the inside of many leaves. (Plate I. fig. 9.)
2. The *lobed* (Plate I. fig. 2. *f*); in the inside of the leaf of Nuphar luteum, Lilium candidum, Vicia Faba, &c.: in this form of cellular tissue the vesicles are sometimes

oblong, with a sort of leg or projecting lobe towards one end; and sometimes irregularly triangular, with the sides pressed in and the angles truncated. They are well represented in the plates of Adolphe Brongniart's memoir upon the organisation of leaves, in the *Annales des Sciences,* vol. xxi.

3. The *cubical;* in the epidermis of some leaves, in the bark of many herbaceous plants, and frequently in pith. (Plate I. fig. 13.)
4. The *prismatical;* in some pith, in liber, and in the vicinity of vessels of any sort. (Plate I. fig. 6.)
5. The *cylindrical* (Plate I. fig. 8. *a*); in Chara; this has been seen by Amici so large, that a single vesicle measured four inches in length and one third of a line in diameter. (*Ann. des Sciences,* vol. ii. p. 246.)
6. The *fusiform,* or the oblong pointed at each end; in the membrane that surrounds the seed of a Gourd. (Plate I. fig. 5.)
7. The *muriform;* in the medullary rays. This consists of prismatical bladders compressed between woody tissue or vessels, with their principal diameter horizontal, and in the direction of the radii of the stem. It is so arranged that when viewed laterally it resembles the bricks in a wall; whence its name. (Plate I. fig. 7.)
8. The *compressed;* in the epidermis of all plants. Here the bladders are often so compressed as to appear to be only a single membrane. (Plate I. fig. 2. *a;* Plate III. fig. 3, 4, &c.)
9. The *sinuous;* in the epidermis, and also sometimes beneath it, as in the leaf of Lilium candidum. (Plate III. fig. 5.)
10. The *stellated;* where the cells are so deeply lobed at the angles as to leave open passages between them, as in the stem of Eriophorum vaginatum. Plate III. fig. 2. is an approach to this structure.
11. The *tabular;* as in the epiphlœum of many plants.

Cellular tissue is frequently called *Parenchym.* Professor Link distinguishes *Parenchym* from *Prosenchym;* referring to the former all tissue in which the bladders (Plate I. fig. 1, 3, 6, 7 &c.) have truncated extremities; and to the latter,

forms of tissue in which the bladders taper to each end, and consequently overlap each other at their extremities.

Meyen has *Merenchym*, for ellipsoidal and spheroidal cells; *Parenchym* for angular cells; and *Prosenchym* as above described.

Fibro-cellular Tissue is that in which the sides are composed either of membrane and fibre together, or of fibre only. Link calls all such tissue *spiroid*.

The first observation of this kind with which I am acquainted is that of Moldenhauer, who, in 1779, described the leaves of Sphagnum as marked by fibres twisted spirally (*fig.* 3. *a*, p. 26.) In November, 1827, I described the tissue of Maurandya Barclayana as consisting of bladders formed of spiral threads crossing each other, interlaced from the base to the apex, and connected by a membrane. A few other solitary cases of this kind of tissue had subsequently been observed when the investigations of a modern anatomist suddenly threw an entirely new light upon the subject.

Instead of being very rare, cellular tissue of this kind appears to be quite common; it has been already mentioned as existing in the leaves of Sphagnum; it is also found in the pith of Rubus odoratus. I originally discovered it in the parenchym of the leaves of Oncidium altissimum, and in the coat of various seeds. Mr. Griffith detected it abundantly in the aërial roots of Orchids, where in fact it is extremely common, and Purkinje has shown, by a series of excellent observations and drawings, that it constitutes the lining of the valves of almost all anthers.

Schleiden would seem to regard the spiral condition of the interior of cells as a universal fact. But, although we know of nothing to support this strong opinion, which seems to result from hypothetical considerations, his statements respecting some instances, in which it certainly occurs, are interesting. After adverting to the spiral structure known to exist in the reproductive organs of Liverworts and Scale-Mosses, he shows that it is not less strikingly developed in the organs of vegetation of Liverworts (Marchantiaceæ.) The parenchym of the leaf in Marchantia polymorpha and

Fegatella conica consists almost entirely of cells the partitions of which are either distinctly porous or thickened beautifully with network.

"Among mosses, Dicranum Schraderi, spurium, &c., are distinguished by having the cells of the leaves very thick-sided, and pierced by wide or funnel-shaped pore canals. Still more conspicuously do these spiral and porous formations display themselves not only in Sphagnum, but in the whole group of Leucophaneæ. The structure of the cells of Sphagnum, Leucobryum vulgare (Dicranum glaucum) and Octoblepharum albidum has been pointed out by Mohl. The great pores, which in the older state of the leaf become real holes, also occur in Octoblepharum cylindricum, Didymodon sphagnoides, and in Leucobryum minus, albidum, and longifolium. In fact, all the mosses called Leucophaneæ are characterised, like Sphagneæ, by peculiarities in the structure of the leaf, which consists of two different species of cells, some narrow and filled with chlorophyll, others wider, transparent, and perforated with pores, which afterwards pass into holes." (See *Annals of Natural History*, vol. v. p. 73.)

It may, however, happen that a spiral appearance is given to cellular tissue, without the actual presence of any spiral structure, of which an example is given by Dr. Willshire.

In the twisted seed-vessel of Loasa lateritia, he found that the cellular tissue consisted of long cells, "closely approaching to, or even apparently identical with, one portion of the woody tissue of the stem, and marked longitudinally by a single row of dots or pores exactly like those on the ducts of the vascular system of the plant: the fibres of the different layers crossed each other obliquely, so that when two layers are examined under the microscope the structure is netted, and between each mesh a single pore is seen." (*Annals of Natural History*, vol. x. p. 5.)

The principal varieties are these:—

A. *Membrane and Fibre combined.*

1. Fibres twisted spirally, adhering to a spheroidal or angular membrane, and often anastomosing irregularly, without the spires touching each other. (Plate I. fig. 12.) This

is what is found in Oncidium altissimum leaves, in the aërial roots of some Orchids, in the lining of many anthers, and is what Mohl has figured (*Ueber die Poren, &c.* tab. 1. fig. 9), from the pith of Rubus odoratus. It approaches very nearly to the nature of spiral vessels, hereafter to be described, and appears only to be distinguishable by the spires of the fibres not being in contact, being incapable of unrolling, having no elasticity or tenacity; and by the bladders not being cylindrical and tapering to each end, but spheroidal. It is easily examinable in Pleurothallis ruscifolia, and forms upon the side of the cells elevations which give them a beautifully pitted appearance when cut across. In the subcutaneous parenchym of the leaves of this plant the fibres of one cell are placed exactly opposite those of the next cell, so that sections of the walls exhibit double depressions and elevations all along the line, so regular that, unless a very good microscope is used, they appear to form open passages from one cell to the other.

2. Fibres crossing each other spirally, and forming a reticulated appearance by their anastomosing within oblong bladders. Of this nature are the reticulated cells of the seed-coat of Maurandya Barclayana, Wightia gigantea, and the like. (Plate I. fig. 11.) In the seed of Soymida febrifuga there lies in the middle of the wing a thick stratum of fibro-cellular bodies, which would be regarded as spiral vessels if they were longer and more cylindrical; but which seem to belong to this form of fibro-cellular tissue.
3. On the surface of the seed of the almond Mr. Quekett observed numerous projecting cells which have very thick parietes: these can be found burst and their contents emitted; in fact they look more like eggs of some minute insect, which however they are not, because if the seeds of unopened almonds are examined, these bodies will be found there likewise: they appear to be analogous to the cells on the seeds of Cobæa scandens, which Don describes as *mealiness*, but which are instead, most beautiful examples of fibro-cellular tissue.

4. Fibres running spirally close together, except at certain places where they separate and leave between them small spaces, which appear like dots.
5. Fibres running spirally, but completely grown together, except at certain places where they separate and leave small dot-like spaces. This and the last have been noticed by Mr. Valentine in Orchideous plants, and have been extremely well figured by Slack. (*Trans. Soc. Arts*, vol. xlix. *t.* 6. *f.* 5, 6.)
6. Fibres running straight along the sides of truncated cylindrical cells in the anthers of Richardia africana (Calla æthiopica) and many other plants. (Plate I. fig. 13.)
7. Fibres running transversely in parallel lines round three of the sides of prismatical right-angled cells, in the anthers of water-lilies (Nymphæaceæ), &c.
8. Fibres very short, attached to the sides of cells of various figures, to which they give a sort of toothed appearance, as in the anther of Phlomis fruticosa and other Labiates. (Plate I. fig. 15.)

The last three were first noticed by Purkinje.

9. The fibre twisted spirally, in the membranous tubes that form the *elaters* of Jungermannia, apparently constitutes another form of tissue of this order (Plate I. fig. 17), and has recently been found by several observers among Fungals in the genus Trichia.

B. *Fibre without Membrane.*

It is not improbable that this form is always in the beginning of its growth composed of membrane. Mirbel has shown that the curious cells which line the anther of the common gourd are continuous membranes till just before the expansion of the flower, when they very suddenly enlarge, and their sides divide into narrow ribands or threads, curved in almost elliptical rings which adhere to the shell of the anther by one end; these rings are placed parallel with each other in each cell, to which they give an appearance like that of a little gallery with two rows of pilasters, the connecting

arches of which remain after the destruction of the roof and walls. According to the observations of Schleiden, the formation of fibre never takes place independently of membrane, but occurs in the interior of cells, whose membrane was originally quite simple. He regards Corda's statements to the contrary (*Ueber Spiralfaserzellen*, 7 and 8), as formed upon imperfect observations. He says that cells always attain their full size before the fibre appears, and he regards its formation as a part of the process of lignification. In the beginning he states that each cell is filled with starch, rarely with mucus or gum. By degrees the starch is always converted into the latter; this becomes changed, and, as it would seem, always from without inwards, into jelly. This jelly changes at its surface into a spiral fibre of variable width, which either does or does not adhere to the sides of the cells, and which may be supposed to owe its spiral direction to the course taken by a current setting between the side of the cell and the central mass of jelly. This seems to be shown by Collomia linearis described below, in which the mucus is not precipitated in the form of an inclosing membrane, and by the curious hairs of Acanthads, our knowledge of which is due to Mr. Kippist. In these plants various conditions occur between a tubular cell without spiral, and a spiral thread without apparent tube. In Blechum Brownei, Ruellia littoralis, &c., will be found tubes without spiral, but discharging mucus through a hole in their end; in Ruellia formosa, a slight appearance of spiral makes its appearance in a mucus tube; in some Hygrophilas the spirals are broken, or at least appear within tubes in the form of rings, and in Acanthodium, where the spiral acquires a high development, the cell-membrane is hardly discoverable.

The following are the more important varieties:—

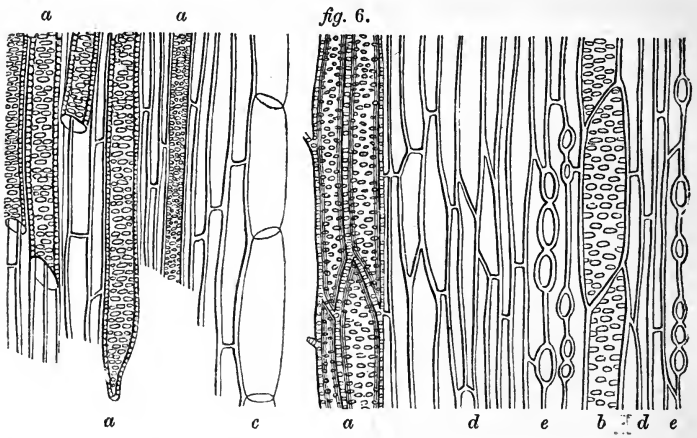
1. Spiral fibres repressed by mucus, but having sufficient elasticity to uncoil when the mucus is dissolved, and then breaking up into rings. (Plate I. fig. 16.) These are what are found in the seed-coat of Collomia linearis. They approach spiral vessels so very nearly, that when I originally discovered them I mistook them for such. They are known by their depressed figure when at rest,

by the want of an inclosing membrane, and by their brittleness when uncoiled.

2. Fibres short, straight, and radiating, so as to form little starlike appearances, found by Purkinje in the lining of the anthers of Polygala Chamæbuxus, &c. (Plate I. fig. 19.)
3. Fibres originating in a circle, curving upwards into a sort of dome, and uniting at the summit, observed by the same anatomist in the anthers of Veronica perfoliata, &c.
4. Fibres standing in rows, each distinct from its neighbour, and having its point hooked, so that the whole has some resemblance to the teeth of a currycomb, in the anthers of Campanula; first noticed by Purkinje. (Plate I. fig. 18.)
5. Fibres forming distinct arches, as seen in the anthers of Linaria Cymbalaria, &c. by Purkinje. (Plate I. fig. 4.)

SECT. II.—*Of Pitted Tissue, or Bothrenchym.**

fig. 6.



This, which has had a variety of names, (*Tubes poreux, Vaisseaux en chapelet, Tubes corpusculiféres,* Vasiform Tissue, Dotted Ducts,) consists of tubes, often of considerable size, appearing when viewed by transmitted light as if riddled

* Βοθρος, a little pit.

full of holes. Upon a more accurate inspection, however, it is found to receive that appearance from its sides being filled with little pits sunk in the thickness of their lining. (See Plate II. fig. 2.)

By far the most complete account which we possess of this kind of structure, is due to the accurate researches of Professor Mohl, whose remarks I quote at length from Mr. Berkeley's translation in the *Annals of Natural History*, vol. ix. After adverting to the mistake committed by some anatomists in regarding the structure of pitted tissue as being extremely uniform, he proceeds to describe various very distinct forms.

In the first instance, however, he points out the important fact, that the pitted tubes of most plants do not possess an uniform structure all round, but the condition of their walls is materially affected by that of the contiguous organs. The medullary rays in many plants exercise a powerful influence on the structure of the cells of bothrenchym, as in those parts of the tube which are in contact with the medullary rays the pits have an irregular form, want the customary borders, are always situated where only a neighbouring cell is closely pressed, and near where the lateral walls of a neighbouring cell stand perpendicular to them; that, moreover, the pits of two tubes applied immediately the one to the other exactly correspond.

The forms of Bothrenchym, recognised by Mohl, are the following:—

A. Where the walls exhibit no variations, whether standing in contact with other tubes or with cells, being therefore uniformly studded with pits which are surrounded by a border, as in Elæagnus acuminatus, Clematis Vitalba, Broussonetia papyrifera.

B. In which those sides of the tubes which stand in contact with prosenchymatous cells are furnished with equal dots surrounded by a border, but in which the action of neighbouring cells is indicated by the pits on the walls which abut on the cells being placed at greater distances. Such tissue occurs in Bixa Orellana, Acacia lophantha, Sophora Japonica.

C. When, with a more intimate dependence of the tubes on the cells, the walls abutting on other vessels remain thickly studded with pits; only those in contact with prosenchymatous cells present very remote dots, or (at least for considerable distances) none at all. The parts bordering on the medullary rays have simple pits. Such tissue occurs in Sambucus nigra, Betula alba, Aralia spinosa, Corylus Avellana, Populus alba, Alnus incana, Platanus occidentalis, Pyrus Malus, Gymnocladus canadensis.

D. When contiguous cells, which have more commonly the form of parenchym than prosenchym, exhibit pits surrounded by a border on those portions of the walls only which abut on other tubes; those portions, on the contrary, abutting on cells have numerous, large, perfectly borderless pits, resembling those of the parenchym e. g. Cassytha glabella, C. filiformis, Bombax pentandrum, Hernandia ovigera.

E. There is a mere modification of this structure, but a very peculiar one, when the walls which press on another tube are fashioned like scalariform vessels, in consequence of the pits being drawn out into fissures which extend the whole breadth of the tube, while those walls which are contiguous to cells only produce large borderless pits. This form is beautifully developed in Chilianthus arboreus and Cynanchum obtusifolium. In a less degree the same phænomena are exhibited by Vitis vinifera in the walls contiguous to vessels.

Most bothrenchym may be referred to one of the heads just enumerated. There is, however, in addition, a series of forms in which the intervals between the rows of pits are not level, but marked on the inside wall with a spiral line.

These tubes are to ordinary bothrenchym what the dotted tubes of Taxus are to other Conifers. In this kind of tissue not only do we find variations in the distribution of the pits similar to those just enumerated, but other differences occur, depending upon the presence of spiral threads in a part or the whole of the tubes. In some plants we may, for instance, distinguish, though not very accurately, greater and smaller tubes which are not always alike forming bundles, more especially on the inner part of annular rings; and near such

bundles, consisting of large tubes, lie others of a smaller calibre, approaching more to the form of prosenchym. These I shall distinguish, in what follows, by the name of minor tubes.

This kind of Bothrenchym may be arranged as follows :—

F. Bundles of tubes covered with bordered pits, the major having smooth walls; the minor, spiral threads between the rows. Morus alba, Ulmus campestris, Clematis Vitalba.

G. Bundles of vessels, closely pitted, with fine threads between the rows of pits, Hakea oleifolia.

H. The major tubes pitted, the minor without pits; the walls of both coated inside with spiral threads. Daphne Mezereum, Passerina filiformis, Bupleurum arborescens, Genista canariensis.

I. Walls of the tubes which touch other tubes pitted; those which touch cells with distant pits or with none; the walls of both kinds of tubes furnished with spiral threads. Samara pentandra, Tilia parvifolia, Æsculus Hippocastanum, Acer Pseudo-platanus, Cornus alba, Ilex Aquifolium, Cratægus oxyacantha, Prunus Padus, P. virginiana.

Mohl observes, that a question may be raised as to whether all these forms of pitted tissue are to be regarded as bothrenchym, or those tubes only which have bordered pits on all sides, the rest being regarded as "mixed vessels," or whether the foregoing differences are to become the foundation of more distinctions among vessels. He very rightly shows that the first question only can be answered in the affirmative. All these forms of tissue possess an important common character in the structure of their bordered pits, by which they are easily and decidedly distinguished.

The tubes of bothrenchym exhibit here and there in their length transverse dissepiments, now very distant, now close together; these are either absorbed in the course of the formation of the tubes, or remain pierced with a circular hole, or "transverse fissures placed one above the other so as to resemble the walls of a scalariform vessel." The last condition is only known in partitions which have an oblique position; such fissures are analogous to the holes or gratings

which are generally formed in order to secure a free communication between the cavities of tubes placed end to end.

It has been incorrectly said by Bischoff that tissue of this kind is an alteration of a spiral vessel, whose fibre is broken into short pieces, which stick to the sides of the tube and cause the pitted appearance. Mr. Slack adopted his idea: he considered the dots to be transparent spaces in the sides of the cells, and caused by the separation, at intervals, of a spiral fibre whose convolutions are partially and firmly united in the spaces between the dots; and he represents a case of vasiformì tissue from Hippuris in illustration of his position. But I have sought in vain for any proof of the correctness of these views.

I think it was Du Petit Thouars who first showed bothrenchym to be formed by the junction end to end of truncated cells, whose dissepiments are gradually absorbed. The most detailed account of its origin is given by Mohl to the following effect:—

Bothrenchym appears when first developed, as rows of large, cell-like, perfectly closed tubes, whose skin is thin and perfectly uniform, and every one possessing a Cytoblast. At a later period, on the walls, especially those impinging on other tubes, appears a delicate fibrous net-work. A further inspection shows that this does not (as might have been at first believed) depend on fibres deposited on the inner walls of the tube, but that the meshes of the net correspond with the future borders of the pits, and therefore indicate the cavities which lie between the tubes; that the seeming fibres which surround the meshes are formed by the places of the walls of the vessel which remain in contact with the neighbouring organ; and that at this time, as well as during the whole process of development, the tubes are filled with sap, not with air as Schleiden asserted. Shortly after the appearance of these cavities the first trace of the pit over each of them is indicated by a lighter circle, and now and then, by means of the further thickening of the walls, the formation of the tubes speedily arrives at completion, the transverse dissepiments being at the same time absorbed.

From what has been already stated as to the form of the

canals of the pits, it is evident that the apertures of the secondary coats are much larger, much more drawn out in the direction of their major axis into the form of fissures, the nearer they lie to the centre of the tube ;—this shows that the different secondary coats of the same tube do not accurately agree in their form. In some plants, as in Bombax pentandrum this circumstance is indicated merely by a slight conical enlargement inwards of the pit canal. It becomes more remarkable in Cassytha glabella and especially in Laurus Sassafras, Aleurites triloba, Elæagnus acuminata or Clematis Vitalba. In these plants the canal in the deposit next the outside resembles a pit which is shorter than the border, while, on the contrary, that of the succeeding coats is extended into such a long slit, that it is not merely longer than the border below it, but the slits frequently run into one another, blending the canals of many pits. The interior layers, therefore, represent skins, which are imperfectly divided into broad threads by long and short fissures. It is to be remarked here, that the direction of the fissures of the inner layers does not always perfectly agree with the direction of the major axis of the canals of the pits, but intersects it at a small angle. This will be the less surprising if we remember that the threads in Taxus which form the innermost layer of the vessels in that plant, run sometimes in an opposite direction to the spiral line in which the major axis of the dots lies; and that the liber-cells of Dogbanes (Apocynaceæ) are composed of coats whose spiral striæ exhibit equally a different direction of volution. I find the greatest degree of difference between the outer and inner coats of the bothrenchym in Tilia, Daphne and the other plants mentioned above, in which a perfect division of the inner membrane of the vessel into spiral threads exists. (See *Annals of Natural History*, vol. ix., for further details and figures illustrating these descriptions.)

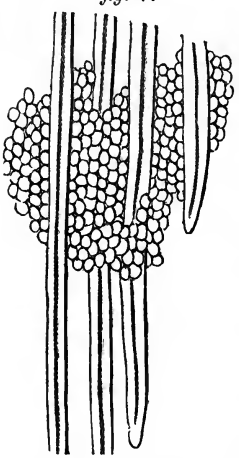
Sect. III.—*Of Woody Tissue, or Pleurenchym.*

This, which Meyen calls *Pleurenchym*, consists of very slender, tough, transparent, membranous tubes, tapering

acutely to each end, lying in bundles, and, like the cellular tissue, having no obvious communication with each other, except by invisible pores. Slack states, that the tubes are often met with open at their extremities; "which probably arises either from the membrane being obliterated where it was applied to another fibre, or ruptured by the presence of an adjoining tube, as we sometimes find the conical extremity of another tube inserted into the aperture."

Many vegetable anatomists consider it a mere form of cellular tissue, in a lengthened state. However true this may be in theory, woody tissue may be known by its toughness and extremely attenuated character. The distinction between cellular and woody tissue is particularly well seen in the long club-shaped aërial radicle of Rhizophora Candelaria. It there consists of large, very long, transparent tubes, lying imbedded in fine brownish granular matter, which is minute cellular tissue (*fig.* 7.)

fig. 7.



Usually it has no markings upon its surface, except occasionally a particle or two of greenish matter in its inside; but sometimes it is covered with spots that have been mistaken for pores, and which give it a peculiar character (Plate II. fig. 3. 5. and 20.); and I have remarked an instance, in Oncidium altissimum, of its having tubercles on its surface. It often contains amylaceous granules in abundance. Generally, while cellular tissue is brittle, and has little or no cohesion, woody tissue has great tenacity and strength; whence its capability of being manufactured into linen. Every thing prepared from flax, hemp, and the like, is composed of woody tissue; but cotton, which is cellular tissue, bears no comparison as to strength, with either flax or hemp.

Alphonse De Candolle gives the following as the result obtained by Labillardière, as to the relative strength of different

organic fibres. He found that, in suspending weights to threads of the same diameter,

Silk supported a weight equal to . . .	34
New Zealand flax	$23\frac{4}{5}$
Hemp	$16\frac{1}{3}$
Flax	$11\frac{3}{4}$
Pita flax (Agave Americana)	7

That even the most delicate woody tissue consists of tubes, may be readily seen by examining it with a high magnifying power, and also by the occasional detection of particles of greenish matter in its inside. A very different opinion was nevertheless once held by some physiologists, who thought that woody tissue is capable of endless divisibility. "When," says Duhamel, "I have examined under the microscope one of the principal fibres of a pear tree, it seemed to me to consist of a bundle of yet finer fibres; and when I have detached one of those fibres, and submitted it to a more powerful magnifying power than the first, it has still appeared to be formed of a great number of yet more delicate fibres." (*Physique des Arbres*, i. 57.) To this opinion Du Petit Thouars assents, conceiving the tenuity of a fibre to be infinite, as well as its extensibility. (*Essais sur la Végétation*, p. 150.) These views arose from the use of bad microscopes; under low powers of which such appearances as Duhamel describes are visible; but with modern glasses, and after maceration, each particular tube can be separated with the greatest facility. Their diameter is often very much less than that of the finest human hair; the tubes of hemp, for example, when completely separated, are nearly six times smaller. It must, however, be observed, that the fibres of this plant, as used in linen-making, are by no means in a state of final separation, each of the finest that meets the naked eye being in reality a bundle of tubes. While some do not exceed $\frac{1}{3000}$ of an inch in diameter, others have a diameter as considerable as that of ordinary cellular tissue itself; in Conifers the tubes are often $\frac{1}{200}$ or $\frac{1}{300}$, and in the Lime they average about $\frac{1}{150}$. Link states (*Elementa*, p. 85.) that they are very large in trees of hot countries. The sides of woody tissue become thickened,

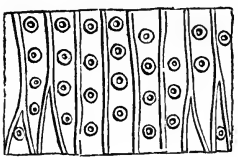
as they advance in age, by the successive deposits of layer after layer in their interior (see *fig.* 1.); this is particularly observable in the liber, and hence, perhaps, the reason why the toughest kinds of fibre are obtained from that part.

There are two distinct kinds of Pleurenchym :—

1. That in which the walls are not occupied with either granules or glands sticking to them, or in which the former are of very rare occurrence (*fig.* 7.) This is the finest and the commonest of all; and is also the most genuine state of woody tissue.

2. The second kind of woody tissue is the *glandular*. This has hitherto been examined chiefly in Conifers, in which it uniformly occurs. Its dimensions are more considerable than those of the last-mentioned form, and it has been described as perforated with pores. The marking of the tubes are vesicular, and usually transparent, with a darkened centre (Plate II. fig. 3.), which last is what has been described as a pore, the vesicle itself being considered a thickened rim.

fig. 8.



Kieser figures the glands as pores in Pinewood (*fig.* 8.), in Ephedra, and other cases. They may be most conveniently found by examining with a microscope a thin shaving of common Pinewood (Pinus Strobus), when they will be seen in the form of transparent globules, having a dark centre, and placed upon the wall of the pleurenchym.

The structure of coniferous glands has of late attracted the attention of many anatomists, and, at last, Professor Mohl seems to have discovered their real nature. He states them to be circular spaces, thinner than the rest of the tube, and placed opposite each other, so that when the walls are examined by transmitted light they appear more transparent than the rest of the tube. A plan of this structure is given in a cross section of two tubes in Plate II. fig. 4., where *a a* represent depressions in the centre of the elevation, which depression is supposed to cause the appearance of a central pore. With patience sections may be obtained so as to show the glands in profile, and then they are seen to project con-

siderably above the wall of the tube. In a specimen of Pinus Strobus I have found them surrounded with an irregular elevated rim, as at Plate II. fig. 7. and 8., as if the lining of the tube was growing over them. It is not at all uncommon to find them in what may be supposed a nascent state, merely looking like tumours, with a pit in the middle, as is shown at Plate II. fig. 5.

Schleiden, while he upon the whole admits Mohl's explanation, nevertheless endeavours to refer this case to his idea of a universally spiral direction of secondary deposits. He believes that he has seen, in Pinus sylvestris, the cells of the cambium, even in the youngest annual rings, constantly divided by delicate black lines into narrow spiral bands previous to the formation of pores, (as matter of course with perfect homogeneity of the primary cellular membrane,) and that these, which he regards as the boundaries of adjacent convolutions, first disappear on the formation of pores, or pits, probably glued to one another in the same manner as the cells themselves, whose bounding lines frequently likewise become invisible at a more advanced age; for when he isolated the cells by boiling in caustic potash, even those from the outside layers of the oldest heart wood constantly exhibited more or less distinctly these delicate stripes, and the pores again appeared merely as narrow clefts between two separating spiral coils.

If the discs of coniferous wood are examined with a good eighth of an inch object glass, and a low ocular, they will be distinctly seen marked with concentric circles as represented at Plate II. fig. 6. The highest oculars with a lower objective will not separate the circular lines. M. Valentin, who first noticed the lines (*Repertorium*, vol. i. t. i.), considers them to be the projecting edges of numerous layers of woody matter concentrically deposited round a space which they gradually close up, except a narrow opening into an air chamber, the layer next the centre being the youngest. I have not succeeded in obtaining any section which will show this structure.

It has been imagined that this glandular Pleurenchym is confined to Gymnosperms, but Dr. Brown long since remarked it in Tasmannia, and Mr. Griffith found it common in aromatic

trees. At Plate II. fig. 20. is a view of it as I see it in Sphærostema.

The nature of the discs has been examined by the late M. Guillemin, who, in a paper laid before the Academy of Sciences, Dec. 19, 1836, considered them to be tumours, and called them *Œdemata*. He supposed them to be flattened vesicles, the central circle being either a pore or minute cell; and he imagined them to be filled with a colourless volatile oil, which changes to turpentine when it has been excluded from the central luminous point. He also adverted to the existence of similar appearances in aromatic woods, especially Drimys chilensis, but said they are not to be confounded with *Œdemata*. (*Comptes Rendus*, iii. 761.) There is, however, no sufficient ground for regarding them as organs of secretion; it is more probable, considering their position, that these circles are analogous to the pits of bothrenchym, and are intended to enable fluid matter to pass in or out of the tubes, which could scarcely take place, except in an inconsiderable degree through their tough thick sides.

The late Mr. E. J. Quekett has given the history of coniferous glands so well, that I extract his observations from the *Linnean Transactions*, vol. xix. p. 150. "The other point that has occasionally been the subject of controversy, is the nature of the discoid bodies on the woody tissue of coniferous plants. These have been supposed by some persons to be glands; by others to be thicker, and by others again to be thinner places in the membrane forming the walls of the woody fibres. Others have asserted that there is a pore in the centre of each disc, which allows of a communication between adjoining fibres. Later observers, however, have shown that none of the above theories are altogether correct, as the discs are not proper to one woody fibre, but are formed between two contiguous fibres, each contributing to the formation of the disc by having a minute depression shaped like a saucer, on its exterior, which corresponds exactly to a similar depression on the contiguous fibre, whereby a small cavity is left between them. These markings or cavities very rarely exist on the sides of the fibres opposed to the pith or bark, but are very numerous on the sides parallel to the medullary

rays. Wherever the markings occur, the saucer-shaped depression is thick at the circumference, and for some distance towards the centre, but in the centre itself there is a spot so extremely thin and minute, that the light, which has to pass through it, becomes decomposed, and the spot looks either green or red, according to the adjustment of the focus.

"Having received from Professor Bailey a specimen of fossil wood which was found at Fredericsberg, in Virginia, I perceived, on submitting it to the microscope, that it would easily break into minute fragments in the direction of the woody fibres, which, when carefully viewed, presented a most beautiful example of casts of woody tissue, with numerous spirals traversing the interior. At various points were arranged the ordinary coniferous dots, and to the outside there adhered small bodies of the same size, which projected beyond the outline of the fibre when seen obliquely, each bearing the precise representation of the coniferous disc. In other parts of the field of view were some of the same bodies detached from the sides of the fibres, which left no doubt that they were casts of the cavities existing in the original plant, and proved the correctness of the view above stated, respecting the nature of these minute circular markings. Besides these siliceous bodies in the fragments of the fossil, there were others of such a shape as to leave no doubt that they were casts of the interspaces between the cells or woody fibres."

Pleurenchym constitutes a considerable proportion of the ligneous part of all plants; it is abundant in liber, and forms the principal part of the veins of leaves, to which it gives stiffness and tenacity.

Sect. IV.—*Of Vascular Tissue, or Trachenchym.*

This consists of simple membranous tubes tapering to each end, but often terminating abruptly, and having a fibre generated spirally in the inside.

Such appears to me to be the most accurate mode of describing this kind of tissue, upon the exact nature of which anatomists have, however, been much divided in opinion;

some believing that the fibre coheres independently of any membrane, others doubting or denying the mode in which the vessels terminate; some describing the vessels as ramifying; and a fourth class ascribing to them pores and fissures, as we have already seen has been done in cellular, pitted, and woody tissue. This has probably arisen from observers having confounded modifications of bothrenchym under the name of vascular tissue, which should be strictly confined to tubes lined with a spiral coating more or less complete.

The spiral fibre is observed to be generally wound to the right; that is to say, the turn of the spiral appears to an observer placed in the interior of the cylinder to mount from left to right. Mohl maintains that this is the usual direction; Schleiden, on the other hand, asserts that left-handed spirals are very common in connection with right-handed. Mohl nevertheless holds to his opinion, and adds that "the volution to the right or left is quite independent of the organisations of the surrounding parts, as is proved by the fact that, in certain cases, not only the spirals of two superposed utricles of the same vessel are wound in opposite directions, but sometimes even in the same vessel, (as in the Gourd), the parts of a spiral fibre separated from each other by rings, are wound in an opposite direction. (*Annals of Natural History*, vol. viii., p. 20.)

There are two principal kinds of vascular tissue; viz. spiral vessels (Plate II. fig. 3. *b*. 9. 11.), and ducts (Plate II. fig. 12. *c. f.* 15. 16. 18. 20.)

Spiral Vessels or Tracheæ are membranous tubes with conical extremities; their inside being occupied by a fibre developed spirally, and capable of unrolling with elasticity. To the eye they, when at rest, look like a wire twisted round a cylinder that is afterwards removed. For the purpose of finding them for examination, the stalk of a strawberry leaf, or a young shoot of the Cornus alba (common dogwood) may be conveniently used; in these they may be readily detected by gently pulling the specimen asunder, when they unroll, and appear to the naked eye like a fine cobweb.

Very different opinions have been entertained as to the

exact structure of spiral vessels. They have been considered to be composed of a fibre only, twisted spirally, without any connecting membrane; or to have their coils connected by an extremely thin membrane, which is destroyed when the vessel unrolls; or to consist of a fibre rolled round a membranous cylinder; or even, and this was Malpighi's idea, to be formed by a spiral fibre kept together as a tube by interlaced fibres. Again, the fibre itself has been by some thought to be a flat strap, by others a tube, and by a third class of observers a kind of gutter formed by a strap having its edges turned a little inwards. Finally, the mode in which they terminate, has been asserted to consist in a gradual transition to cellular tissue.

With regard to the presence of an external membrane within which the spiral fibre is developed, an examination of it externally, by means of longitudinal sections of the surrounding parts, is scarcely sufficient to settle that point. The best mode of examination is to separate a vessel entire from the rest of the tissue, which may be done by boiling the subject, and then tearing it in pieces with the points of needles or any delicate sharp instrument; the real structure will then become much more apparent than if the vessel be viewed in connection with the surrounding tissue. From some beautiful preparations of this kind by Mr. Valentine and Mr. Griffith, it was long since proved that the membrane is external: in the root of the Hyacinth, for example, the coils of the spiral vessel touch each other, except towards its extremities; there they gradually separate, and it is then easy to see that the spiral fibre does not project beyond the membrane, but is bounded externally by the latter, which would not be the case if the membrane were internal: a representation of such a vessel is given at Plate II. fig. 9. Another argument as to the membrane being external may be taken from the manifest analogy that a spiral vessel bears to that form of cellular tissue (page 52), in which a spiral fibre is generated *within* a cellule: it is probable that the origin of the fibre is the same in both cases, and that its position with regard to the membrane is also the same. Longitudinal sections, moreover, of spiral vessels may be obtained, and then it is manifest that the fibre

is internal, because it projects beyond the inside of the vessel, at every turn. Mr. E. J. Quekett proved this by the evidence derived from fossil Palm-wood: he observed that a portion of this substance readily broke down into minute fragments, which, on examination under the microscope, were seen to be composed of cylinders more or less elongated, and minute rounded granules. Round the cylinders was wound a perfect screw (with either a single or compound helix) fashioned from the interior of the spiral vessel, and thus affording the most satisfactory evidence that the spiral fibre is really formed in the interior of the vessel, as most recent observers have maintained. (*Annals of Natural History*, vol. xv., p. 495.)

It is more difficult to determine whether the fibre is solid, or tubular, or flat like a strap; and Amici has even declared his belief that the question is not capable of solution with such optical instruments as are now in use. When magnified 500 times in diameter, a fibre appears to be transparent in the middle, and more or less opaque at the edges; a circumstance which has no doubt given rise to the idea that it is a strap or riband, with the edges either thickened, according to De Candolle, or rolled inwards, according to Mirbel. But it is also the property of a transparent cylinder to exhibit this appearance when viewed by transmitted light, as any one may satisfy himself by examining a bit of a thermometer tube. A better mode of judging is, perhaps, to be found in the way in which the fibre bends when the vessel is flattened. If it were a flat thread, there would be no convexity at the angle of flexure, but the external edge of the bend would be straight. The fibre, however, always maintains its roundness, whatever the degree of pressure that may be applied to it. (Plate II. fig. 10.) This I think conclusive as to the roundness of the fibre; but it does not determine the question of its being tubular or solid. Bischoff, who has investigated the nature of spiral vessels, asserts (*De verâ vasorum plantarum spiralium Structurâ et Functione Commentatio*, 1829), that it is solid, and this almost everybody is now agreed upon. But M. Girou de Buzareingues asserts that it is hollow and contains fluid, and he gives numerous excessively magnified figures to illustrate his statement. Hedwig also long since believed that,

when coloured fluids rise in spiral vessels, he saw them follow the direction of the spires. This last fact may, however, be explained upon the supposition that they rise in the channels formed by the approximation of cylindrical fibres, and not in the fibres themselves; in which case there could be little doubt that the fibres are really solid; and I must declare that I can find no such appearances as those described by M. de Buzareingues; any more than I can the shadow of proof of another statement by the same physiologist, viz., that the fibre often runs *between* two cylindrical tubes, so that there is not only an outer membrane, but an inner one also. He adds that the inner tube contains air, but that fluid is lodged in the space between the two tubes. Such observations cannot be verified, because the learned author on no occasion names the plants in which he has remarked these peculiarities of structure; and as they have hitherto escaped the most skilful vegetable anatomists, they can only be regarded as singular errors caused by insufficient investigation.

Link contends, that the fibre, although simple at first, soon forks and forks again, and that the branches thus produced all follow the direction of the spire.

Schleiden regards the spiral as always originally consisting of two bands, corresponding to an ascending and descending current of organisable matter; and he believes the extremities of the bands to pass into each other at the end of the cells, and at a very early period, in most cases, to cohere into a single band. I cannot say that I have ever been able to verify this conjecture.

The termination of spiral vessels is, beyond all doubt, conical. This was stated by Nees Von Esenbeck, in his *Handbuch der Botanik*, published in 1820; and in 1824 Dutrochet asserted, that they end in conical spires, the point of which becomes very acute; but one would not suppose, judging from the figure given by the latter writer, that he had seen the terminations very clearly. If the point of a spiral vessel in the Hyacinth (Plate II. fig. 9.) be examined, it will be seen that the end of the spiral fibre lies just within the acute point of the vessel, and that the spires become more and more relaxed as they approach the extremity, as if

their power of extension gradually diminished, and the membrane acquired its pointed figure by the diminution of elasticity and extensibility in the fibre. It is not, however, always in a distinct membrane that the spiral vessel ends. In Nepenthes the fibres terminate in a blunt cone, in which no membrane is discoverable. (Plate II. fig. 11.)*

A spiral vessel is formed by the convolutions either of a single spire, or of many, always turning in the same direction. In the first case it is called *simple,* in the latter *compound.* The simple is the more common. (Plate II. fig. 9.) Kieser finds from two to nine fibres in the Plantain (Musa sapientum.) De la Chesnaye as many as twenty-two in the same plant. There are four in Nepenthes (Plate II. fig. 11.), five in Liparis pendula. In general, very compound spiral vessels are thought to be almost confined to Endogenous plants, where they are very common in certain families, especially Marants, Gingerworts (Zingiberaceæ), and Musads; but their existence in Nepenthes, and, according to Rudolphi, in Heracleum speciosum, renders it possible that future observations may show them to be not uncommon among Exogens also.

In Conifers the spiral vessels have in some cases their spires very remote, and even have glands upon their membrane between the spires. Link speaks of a peculiar kind of vessel found in Coniferous plants "fibris tenuissimis distincta," and calls such spirals *vasa spiralia fibrosa.*

In size, spiral vessels, like other kinds of tissue, are variable; they are generally very small in the petals and filaments. Mirbel states them to be sometimes as much as the $\frac{1}{288}$ of an inch in diameter; Hedwig finds them, in some cases, not exceeding the $\frac{1}{3000}$; a very common size is the $\frac{1}{1000}$.

* A singular change occurs in the appearance of the spiral vessels of Nepenthes, after long maceration in dilute nitric acid, or caustic potash: the extremities cease to be conical and spirally fibrous, but become little transparent oblong sacs, in which the spires of the fibres gradually lose themselves. This alteration, which is a very likely cause of deception, is perhaps owing to the extremities of the fibres being more soluble than the other part, the sac being composed of the confluent dissolved fibres. This is in some measure confirmed by the subsequent disappearance of all trace of fibres in every part of the vessels, under the influence of those powerful solvents.

According to the observations of Link, they may be found of extremely different size in one and the same bundle of tissue in the stem of Canna, the largest being $\frac{1}{500}$, the middle size $\frac{1}{960}$, and the smallest $\frac{1}{2000}$, of an inch in diameter.

An irritability of a curious kind has been noticed by Malpighi in the fibre of a spiral vessel. He says (*Anat.* p. 3.), that in herbaceous plants, and some trees, especially in the winter, a beautiful sight may be observed, by tearing gently asunder a portion of a branch or stem still green, so as to separate the coils of the spires. The fibre will be found to have a peristaltic motion, which lasts for a considerable time. An appearance of the same nature has been described by David Don in the bark of Urtica nivea. These observations are, however, not conformable to the experience of others. De Candolle is of opinion that the motion seen by Malpighi is due to a hygrometrical quality combined with elasticity; and as spiral vessels do not exist in the bark of Urtica nivea, there must be some inaccuracy in Don's remark.

The situation of spiral vessels is in that part of the axis of Exogens which surrounds the pith, and is called the medullary sheath, and also in every part the tissue of which originates from it; such as the veins of leaves, and petals, and of all other modifications of leaves. It has been supposed that they are never found either in the bark, the wood, or the root; and this appears to be generally true. But there are exceptions to this: Mirbel and Amici have noticed their existence in roots; Mr. Valentine and Mr. Griffith have both extracted them from the root of the Hyacinth; and they certainly exist in the roots of many exogens; in the Parsnep and the Beet they are large, and readily extracted entire. I know of no instance of their existence in bark, except in Nepenthes, where they are found in prodigious quantities, not only between the alburnum and the liber, embedded in cellular tissue, as was first pointed out to me by Mr. Valentine, but also sparingly both in the bark and wood. They have been described by myself as forming part of the testa of the seed of Collomia, and Brown has described them as existing abundantly in that of Casuarina. In the former case, the tissue was rather the fibro-cellular, as has been

already explained (p. 55); in the latter, they are apparently of an intermediate nature between the fibro-cellular and the vascular; agreeing with the former in size, situation, and general appearance, but differing in being capable of unrolling. Such tissue is, in fact, very common in the skin of seeds, where also true spiral vessels occur when the skin is traversed by veins. Mr. Quekett observed that, if you place almonds in boiling water, and separate the testa, and while thus softened scrape or remove some of the veins which figure its surface, it will be found that the veins are almost wholly spiral vessels, which are of rather minute dimensions. In the stem of Endogens, spiral vessels occur in the bundles of woody tissue that lie among its cellular substance; in the leaves of some plants of this description they are found in such abundance, that, according to De la Chesnaye, as quoted by De Candolle, they are collected in handfuls in some islands of the West Indies for tinder. The same author informs us that about a drachm and a half is yielded by every Plantain (Musa), and that the fibres may be employed either in the manufacture of a sort of down, or may be spun into thread. In Coniferous plants they are few and very small, and in flowerless plants they are for the most part altogether absent; the only exceptions being in Ferns and Lycopods, orders occupying a sort of middle place between flowering and flowerless plants: in these they no doubt exist. The late Mr. Griffith has succeeded in unrolling them in the young shoots of Lycopodium denticulatum, and Mr. Quekett in Diplazium seramporense.

Dr. J. W. Griffith has described a peculiar modification of the true spiral vessel in the petioles of some British ferns.

These tubes are described as being situated in bundles at tolerably regular distances from the axis and from each other, surrounded by the cellular system of the petiole. In the younger petioles they are mixed with spiral vessels, but these are rarely found in the older ones. Their transverse section shows them to be cylindrical or elliptical, not angular nor solid. They are usually of a yellowish brown colour, terminating in acute extremities, which become more obtuse as their age advances. In situ their terminations overlap

one another. Their surfaces are studded with small elliptical markings or dots, not extending far across the tube, but arranged in parallel lines; these dots are rarely exactly opposite each other, so that the axis of any dot in one row rarely coincides with that of any other in the next. They have no tubular nor rimmed margin. Dr. Griffith further states that, on some of the torn edges, projecting solid fibres may be seen leaving spaces between them corresponding to the dotted parts, and sometimes on their edges may be seen the fragments of the lacerated membrane filling up the dots, thus proving that these tubes are composed of two coats, one of united fibres, the other delicate and membranous. In the older petioles the tubes are often continuous at their extremities, but in the younger they are not. When these tubes are examined in the dried state, the delicate membrane filling up the dots is said to disappear, leaving a perfect foramen. The dots are situated obliquely on the walls of the tubes, so that if the upper and under surfaces be brought into focus under the microscrope immediately after one another, or the focus of the object-glass be made to correspond to the centre of the tube, so as to have both surfaces indistinct but still perceptible at the same time, the dots cross one another, showing their arrangement to be spiral. When they are stretched *they do not break but uncoil,* as if the tube were formed by a band of four or five spiral fibres united at the margins. Their terminal points are situated on one side so as to make the end appear cut off obliquely. Dr. Griffith finds these tubes always to contain air, except during their earliest periods. Tubes of a similar kind have been figured by Link from ferns (Aspidium, Polypodium, &c.), but they appear to Dr. Griffith to differ from those now described in having a beaded margin and in the dots being opposite each other. These tubes, it is remarked, are not true ducts, inasmuch as they uncoil without breaking, and contain air; they cannot be considered as any form of woody tissue for the last-mentioned reason, as well as because the dots have a spiral arrangement. They are not scalariform vessels, as their markings do not extend across the tube, nor are they angular. They agree with spiral vessels in, 1. terminating in

pointed extremities; 2. containing air; 3. being composed of a fibre or fibres and a membrane; 4. uncoiling elastically. So that, although not actually spiral vessels, in consequence of the edges of the fibres not being free but adherent, Dr. Griffith regards them as being undoubtedly formed from them, and performing precisely the same physiological functions. (See *Annals of Natural History*, vol. 10, p. 169, where these appearances are figured.)

Some have thought that the spiral vessels terminate in those little openings of the epidermis called stomates; but there does not seem to be any foundation for this opinion.

Ducts (Plate II. fig. 12. and 15.) are membranous tubes, with conical or rounded extremities; their sides being marked with transverse lines, or rings, or bars, and being incapable of unrolling without breaking.

These approach so nearly to the spiral vessel that it is impossible to doubt their being a mere modification of it. Some writers confound all the forms of ducts, and even bothrenchym itself, under the common name of spiral vessels, but it is more convenient to consider them as distinct, not only on account of their peculiar appearances, but because they occupy a station in plants in which true spiral vessels are not often found; and it is therefore probable that their functions are different. They vary between the $\frac{1}{400}$ and the $\frac{1}{800}$ of an inch in diameter.

The forms of the duct seem reducible to the following varieties:—

1. The *Closed* (Plate II. fig. 15.), which are absolutely the same as spiral vessels, except that they will not unroll.
2. The *Annular* (Plate II. fig. 12. *d*). These are well described by Bischoff as being formed of fibrous rings, placed at uncertain intervals; or, to speak more accurately, they, like spiral vessels, are formed of a spiral thread, but it often separates into a number of distinct rings. These rings are included within a membranous tube, by which they are held together. Annular ducts are common in the soft parts of plants, especially in such as grow with much rapidity; in the Garden Balsam they

are particularly abundant. They are among the largest kinds of vessels.

3. The *Reticulated* (Plate II. fig. 12. *f*). In these the spiral fibre, instead of separating into a number of distinct rings, is continuous in some places, and anastomoses in others, so as to form a sort of netted appearance. Vessels of this kind, like the last, are found in the stem of some herbaceous plants; as, for example, the Garden Balsam, in which they may be seen in a great variety of states.

Some anatomists have added to the varieties above enumerated, what they call strangulated vessels (*vaisseaux en chapelet* or *étranglés, corpuscula vermiformia, vasa moniliformia*). These are determined by Bischoff to be mere accidental forms, caused by their irregular compression, when growing in knots or parts that are subject to an interrupted kind of development. They may be found figured in Mirbel's *Elemens*, tab. x. fig. 15.; and in Kieser, fig. 56. and 57.; but the best view of their origin and true nature is in Slack's plate, fig. 33., in the Transactions of the Society of Arts, before referred to. Link defines them to be short spiral vessels with attenuated extremities, and regards them, in his latest works, as young spiral vessels, or as the commencement of spiral vessels, which, instead of lengthening, grow together by their ends.

Vascular tissue always consists of tubes that are unbranched. They have, indeed, been represented by Mirbel as ramifying in some cases: but this opinion has undoubtedly arisen from imperfect observation. When forming a series of vessels, the ends of the tubes overlie each other, as represented in Plate II. fig. 15.

There is no doubt that the membrane is obliterated at the place where two vessels touch each other, so that a hole is formed, or that transverse bars remain under the form of a grating: the latter appearance is produced by the remains of the spiral fibre, some of whose convolutions are partially uncovered in consequence of the absorption of the enveloping membrane. By this simple contrivance all the forms of

vascular tissue open into each other at their points of contact, and so become uninterrupted tubes of great length.

The true history of ducts has given rise to much discussion, and is still, in fact, *sub lite;* the arguments of Mohl and Schleiden, which represent the two opinions now current, may be stated thus. (See *Annals of Natural History,* vols. vi. and viii. for transactions of their original memoirs.)

It will be evident from the illustrations already given in the previous pages, that Mohl admits two kinds of secondary deposits in the interior of tissue, a homogeneous or general formation in some cases, whence the bothrenchym arises, and a spiral formation in others. Schleiden, on the contrary, maintains that all deposits, of whatever nature, are spiral. This author, in his famous memoir upon spiral formation, speaks thus of the point at issue. He believes that the difference of opinion in subordinate matters would disappear if the gradual development of individual cells were kept more distinctly in view, and especially if greater attention were paid to the expansion of cells after the appearance of spiral deposits. "Thus," he says, "in all my inquiries into the structure of the ligneous body, I have never contented myself with comparing the parts of different age of the same individual, but have constantly, as far as the material was at my disposal, at the same time pursued throughout a whole year the development of the same annular ring, by repeated observations on the most varied parts of the plants. Much instruction is likewise to be obtained by watching the development of the spiroids in large Monocotyledonous vascular bundles, as, for instance, in Arundo Donax, where, however, we must not merely compare on the same individual the younger with the older internodes, but must examine homologous internodes on several individuals of different age. In this plant the spiroids in the completely formed bundle, stood in a series radiating from the axis to the circumference, and placed between two large pitted vessels. Annular vessels, with the rings furthest from one another, are nearest to the axis of the internode; thence towards the circumference the rings approach closer together, then pass into broad threaded spiral vessels, and these last

into narrow threaded spiral vessels. Now if the history of the development of such a woody bundle be investigated, it is found that the vessels with distant rings were first formed as spiral vessels; that then, during the gradual expansion of the internode to which the vascular bundle belongs, the formation gradually advances towards the exterior, and the last spiral vessel remains a narrow threaded one, merely because the longitudinal expansion of the cells was nearly at an end when the spiral deposit took place. The two so-called porous vessels, on both sides, are, during the whole of this formative process, cylindrical cells, filled with a grumous fluid, and placed over one another, their walls being perfectly simple; and it is only after the expansion in length is terminated, that the pits originate on their walls. At the same period the perforation of their septa takes place according to a law which seems to me pretty general, that horizontal septa, or such as slightly deviate from this position, are only pierced with a round aperture, those with a more diagonal direction with ladder-like or reticulated apertures; and the most oblique merely with the usual pores."

Schleiden conceives that it is from not paying sufficient attention to this progressive development that anatomists have not recognised the true origin of annular ducts, and he thus further explains his own views:—Of all spiroids the annular ducts originate most exactly from those cells in which a spiral deposit is earliest formed, and therefore at a time when they are infinitely small and delicate. This occurs in the outermost internodes of the bud, and every anatomist is aware of the almost insurmountable difficulties which are then opposed to a perfectly satisfactory examination. No doubt, the delicate indications of spirals have been recognised everywhere in this part as being among the earliest instances of formation; but at the moment when the bud begins to develope, the formation usually proceeds so rapidly that the observation of the intermediate stages becomes almost impossible. It was therefore most important to find a plant in which such difficulties exist in a slighter degree, and on which, therefore, the process might be accurately observed. For these inquiries the Campelia Zanonia, *Rich.*, and the subter-

ranean stem of Equisetum arvense may be used with much advantage.

If the very youngest internodes of the buds of the first-mentioned plant be examined, a single extremely delicate and densely-wound spiral vessel is found in each young woody bundle. In older internodes the spires of this vessel are more distant from each other, and near it may be observed an exterior newly-formed narrow-threaded spiral vessel. But if, at this period, the first-formed vessel is examined more attentively, it will be found that all convolutions are not separated in the same manner from one another, but that almost in regular alternation two entire coils adhere firmly, and one convolution is drawn out. In still older internodes the extension is found to be so far advanced, that the free coil loosened from the cell-membrane frequently stretches in the form of a mere band, with a steep ascent from one ring formed of two closed convolutions to another. When the vessels are still further developed, this elongated coil is seen to be corroded by the reabsorbing action of the cell, and all stages of transition are frequently found present in a single duct. Finally, in still older ducts, the connecting spire is perfectly dissolved; and there may be observed on the separate rings the extremities of the original spiral fibre. Schleiden adds that exactly the same process may be remarked in the subterranean rhizomes of Equisetum arvense.

To these statements Mohl replies thus, (see his paper translated, with a plate, in the *Annals of Natural History*, vol. viii. p. 20): "When we examine the fibre of the perfectly developed annular vessel (for which researches I have been accustomed to use the Commelina tuberosa), we find its organisation absolutely analogous to that of the spiral fibre, in the rings being composed sometimes of an apparently homogeneous substance, and sometimes exhibiting traces of a determinate structure. In the broad fibres of C. tuberosa, the fibre frequently exhibits a great number of shallow linear furrows or perfect fissures, forming a net-work of very narrow and elongated meshes. More frequently still these fissures are found in an uninterrupted line in the medial line of the fibre, or they become confluent, and thus divide the ring into two

superposed rings. When this latter division takes place, it generally occurs on every ring of a vessel. Frequently, however, this does not occur; but divided and undivided rings alternate in an irregular manner, the undivided rings being sometimes of equal size, sometimes of half the size of the divided rings, and sometimes of a size very inconsiderable in comparison with the divided rings. The direction of this line of division is parallel to the lateral edges of the ring, so that, by this fissure, the ring is divided into two superposed rings, which sometimes touch and sometimes are placed at a little distance from each other. According to Schleiden, this line of division proceeds from the coils of the spiral fibre being more or less completely soldered together, and always in pairs. We easily perceive that, in this case, the line of partition should be directed spirally from one edge of the ring towards the other, and that it should not be parallel to its edges, but as the latter is constantly the case, we must reject this explanation of the origin of the line of partition.

"In the developed annular vessel, the rings are either entirely isolated, or two or three are joined together in different ways. It not unfrequently happens that the line of partition does not divide the ring throughout the whole of its circumference, but that the two superposed rings are united for a space variable in extent; in which case the parts separted are removed to a greater or less distance from each other, and are placed obliquely to the axis of the vessel. In other cases, and this is the habitual organisation, the rings are removed to a greater or less distance from each other, and are separated by a regular spiral fibre, which, according to the distance of the rings, describes one or more volutions, and frequently even a great number. Of this there are several modifications: very generally from a ring will proceed a spiral fibre of the same width as the annular fibre, the distance of whose coils is nearly equal to that of the rings in the portion of the vessel which exhibits this structure; the other extremity of the fibre being similarly annexed to a complete ring, followed by rings either isolated or again reunited by spiral fibres.

"Very frequently also the spiral fibre, placed between two rings, does not proceed to a junction with the rings, but its extremities become attenuated, and terminate at some distance from the ring. In the stem of the Gourd this is nearly as frequent as the preceding case. Often, also, from two diametrically opposite points of a ring proceed two fibres in a continuous parallel direction.

"Cases are sometimes met with, although rarely, where two rings are united by fibres slenderer than the annular fibre, which generally form a single coil, or at least only a small number of coils. This occurs in a very evident manner in the vessels whose rings are not homogeneous, but where the spiral fibre is divided by several fissures into threads united in net-work. The width of the fibres uniting the different rings presents no exact proportion to the width of the annular fibre, being sometimes about the half of it, sometimes considerably less. The point of union of the spiral fibre with the annular fibre is especially deserving of consideration. When examined with a sufficient magnifying power, we sometimes find that a part of the annular fibre separates itself to ascend in a spiral direction; but that, in general, at the point of junction of the two fibres, the annular fibre does not become thinner, the spiral fibre being attached only to the lateral edge of the annular fibre, which preserves an uniform thickness throughout its entire extent. There are even instances in which this union does not take place in the direction of the spiral, but where the spiral fibre terminates in two divergent branches separating right and left, and confluent with the annular fibre.

"An examination of the proportions above mentioned between the annular fibres and the spiral fibres which unite them must excite doubts of the accuracy of Schleiden's theory of the origin of annular vessels. In fact, the division which takes place in many rings is, as we have seen, nothing less than a proof of the ring being composed of the two united fibres of a spiral fibre; whilst, on the other hand, the direction of this division parallel to the edges of the rings is quite opposed to Schleiden's theory, and shows us that, in these more or less divided rings, we see a transition from the simple ring to two

rings, situated at considerable distances from each other. An organisation entirely analogous is also found in the spiral fibre, for there are spiral vessels traversed in the middle by a narrow fissure, by which the decomposition of the simple spiral fibre into two fibres placed at certain parallel distances is indicated.

"What chiefly militates against the formation of rings by the united spiral coils of a spiral vessel, is the proportion which the rings bear to the spiroïd fibres which unite them. And first, when the organisation of the vessels is very regular, the rings and the fibres are generally of the same width, which could not be the case if the rings were composed of a double twist of the fibre. If, then, the spiral fibres which unite the rings are slender, the width of these fibres bears no exact proportion to the width of the rings, and of the divisions perceived in them; moreover, the fibres are sometimes soldered to the rings, and sometimes separated from them. The spiral fibres, when they are united to the rings, cannot be considered in certain cases, and according to the form of the point of union, as a part of the fibrous mass which forms the ring; this part separating from the ring, and continuing in a spiral direction. I have thought it right to explain these considerations, in the first instance, upon the annular vessels in a state of complete development, because observations made on developed vessels are necessarily more precise and certain than those made on young vessels; not so much on account of the larger size of the developed vessels; but because, in consequence of the greater thickness of their fibres, of the greater distance of these organs from each other, and of the absence of the mucilage with which the young vessels are gorged, these developed vessels present a much clearer contour, and the organisation of their fibres is more easily observed. Doubtless it is true that we ought not to infer from the structure of a developed organ the mode of its development; but the examination of this structure is nevertheless of very great importance in studying the manner of its development, since we always thence obtain the means of proving the truth of any theory propounded on the history of development, a theory which ought not to be in contradiction

with the results of an examination of the developed organ. Now, in the present case this contradiction assuredly exists between the structure of the developed annular vessels and the theory of Schleiden.

"Let us now see what information the examination of the young vessels gives us of the mode of their development. At first I selected the stems of different plants, especially of Tradescantia tuberosa, because Schleiden announced that he had remarked the metamorphosis of spiral vessels into annular vessels in the youngest internodes of subterranean and ascending stems. The results have not been favourable to the theory of Schleiden. For this examination it is not proper to select vessels placed at the interior angle of the vascular bundles, because these pass too rapidly through the phases of their development, and their diameter is also too small; the coils of their fibres being, moreover, at first too close together to allow any observations made upon them to be considered as conclusive. The larger vessels, placed more towards the exterior, present less difficulties in these respects, though here also an unfavourable circumstance occurs, viz., that the rings in the course of their development, in consequence of the feeble longitudinal growth of the vascular utricles, remain very close together, which may, in some cases, render the distinction of the annular and spiral formations in the fibres difficult, and which, in all cases, makes it rather hard to decide whether there does or does not exist between each pair of rings a slender spiral fibre, which is subsequently absorbed. However, I think I have observed with certainty, that from the beginning, and so soon as I could distinguish the fibres on the interior surface of the vascular utricle, under the form of thin, more or less narrow, diaphanous edges, they were not absolutely spiral; but that, as in the developed vessels, they formed either complete isolated rings, or rings intermixed with spiral fibres; so that, with the exception of the thinness of the fibres, and of the small distance of the rings from each other, there is no essential difference observable between them and the perfectly developed vessels.

"The examination of the vessels of the stem not having,

however, furnished me with a perfectly satisfactory result, and my former researches on the roots of Palms and other monocotyledonous plants having shown me the greater facility of studying the development in this organ than in the trunk, I submitted the roots of Tradescantia to a very attentive examination, the results of which I consider to be quite conclusive. The examination of the roots presents this great advantage over that of the stems, that in the larger vessels, placed nearer to the centre, the fibres are not developed until a sufficiently late period, when their longitudinal growth is already terminated. At the period when the fibres of the vascular utricles are developed, these utricles have not only already attained to a considerable size, but the fibres in them are also, from the beginning, arranged at greater distances from each other, and their successive development may be followed in detail, step by step, from one end of the root to the other. This examination is rendered easier in consequence of the vessels being deposited in a very transparent cellular tissue. In these researches I have recognised with the greatest clearness, and with a perfect conformity to what I had previously observed in the roots of Palms, that, from the time when the fibres make their appearance, and when they are still so tender, narrow, and transparent, that it is often only possible to see them with a faint light, they already present all the different modifications of form which are observed in the perfect vessels. We then find, as at a later period, the same alternation of annular, and spiral, and reticulated fibres; but I have never seen the least trace of the formation in all vascular utricles of a spiral fibre whose coils would unite in pairs, and the portions of the spiral fibre serving as the means of union be absorbed; and I consider it as perfectly impossible that this transition of spiral vessels into annular vessels, if it existed, could have escaped me, because in a great number of roots I have followed the vessels from the moment when the utricles presented closed cells with thin parietes, and inclosed a nucleus.

"Hence it results that the development of the annular vessels agrees with the observations made on the perfect vessels. Researches into these two organs show that

annular, spiral, and reticulated vessels afford three different forms, very intimately connected, and passing frequently one into the other; but that they must not be considered as temporary degrees of metamorphosis of the same vascular utricle. It is true that a spiral organisation is the ordinary and normal state in the secondary layers of the vessels; but it is not the only state to be found there. Annular organisation occurs as a primary formation, and presents in some degree an intermediate form between the spiral wound to the left and that wound to the right. Moreover, reticulated organisation is also found primitively, sometimes more nearly resembling the pure spiral, and sometimes the annular form."

To this Schleiden replies that his history of the development of annular vessels applied only to the simplest case, that of rings arising from a single thread; and he is confident that he has not deceived himself in the cases alleged, because his researches were made on vessels which, when mature, are purely annular; so that he could not but believe that he had before him, not mere persistent modifications of structure, but really stages of transition, even though he could not have regarded the observed forms as actually detected in the act of development; not to mention, among other circumstances, that the persistent ring is distinguished by the sharpness of its outline, the firmness and clearness of its substance, from the yellowish gelatinous transitory portion, with its eroded and defaced margin, observed in the moment of dissolution.

In conclusion, he points out a source of error against which observers should be guarded, arising from the formation, after the original fibre, of secondary threads, uniting the primary, but certainly of a different nature; as is proved by their solubility in boiling caustic potash. He also refers, in support of his own views, to the philosophical necessity of limiting the number of principles of interpretation "so long as the impossibility of referring a phenomenon to an old principle does not imperatively require a new one."

The researches of Mohl into the true history of Bothrenchym show that on the sides of some kinds of pitted tissue, included

by him under his division E, the pits extend into horizontal fissures resembling what are called *Scalariform* vessels. This would seem to render it probable that the last-mentioned tissue belongs to Bothrenchym and not to Parenchym. Scalariform tissue, which is only found in Ferns, consists of angular tubes, whose sides are marked by transverse fissures, or bars, which scarcely reach the angles, where all interruption of continuity ceases, the angles looking under the microscope like transparent lines parallel to the axis of the tube. (Fig. 9, and *Elements of Botany*, fig. 37). This is just like the

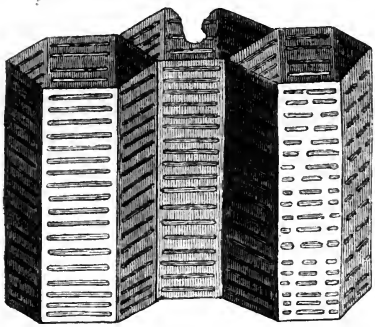


fig. 9.

structure which Mohl represents as belonging to the Bothrenchym of Chilianthus arboreus. (*Ann. Nat. Hist.*, ix, t. 8, f. 2). But as Mr. Quekett says he has succeeded in unrolling the scalariform vessels of Diplazium seramporense, it is as well to regard them as a modification of the spiral vessel until their true nature shall have been better ascertained.

Dr. J. W. Griffith, who figures this kind of tissue in the *Annals of Natural History*, vol. ii, t. 4, p. 22, gives the following explanation of its origin; it is, however, to be borne in mind that he includes under the name of dotted ducts not only bothrenchym, as limited in this work, but also the modifications of spiral vessels to which the name of ducts is here restricted:—"When a spiral vessel has formed in a young plant, the rapid growth of the stem induces considerable pressure of the surrounding parts; the consequence is, that the convexity or parts of the surrounding vessels or cells opposite to the spiral vessel are pressed firmly against it, whilst

opposite the intercellular and intervascular spaces the pressure is much less; thus the fibre within the compressed spiral is bent into as many sides as there are surrounding and pressing vesicles or vessels. Accordingly, if the spiral fibre be examined at this period, it will be found bent as above mentioned, and the natural curve of the fibre straightened. Opposite the intercellular or intervascular spaces, *i. e.* at the bendings of the fibres, the latter become firmly adherent to the membrane, thickened and united to the fibres above and below. These thickened portions form the line of space running between the rows of dots. The dots themselves are formed by the spaces left between the portions of the fibres opposite the convexity of the surrounding cells and vessels. Thus, when we examine the tubes at this stage, we find the membrane and fibre united so firmly, that they are with great difficulty separated. The vegetable substance which fills up the intercellular spaces often also becomes firmly adherent to the membrane and fibre, so that, when we dissect out one of these tubes from the surrounding parts, we often find the remains of adherent portions which existed opposite the intercellular spaces; therefore the number and arrangement of the dots must depend entirely upon the surrounding vessels and cells. When the compressing and compressed tubes are equal in size, the dots extend nearly across the face or opposed side of the tube; and when several small tubes and vessels compress a spiral, so as to convert it into a dotted tube, the dots will be small and numerous. The observation of Schleiden, that 'in consequence of the deposition of formative substance, the pore appears the rounder the more the cell is developed,' is, I think, incorrect; I believe the reverse to be correct. The examination of the young and old stems of any plant containing these vessels will prove this. If the fibre be separated from the surrounding parts in the early stages, it will be found bent and thickened at the bendings; and oftentimes we can find portions of membrane, &c. adhering as above mentioned. These vessels are generally observed in plants whose growth is rapid, so that in older stems we cannot expect to find the arrangement persistent; but in a large number of plants it can readily be perceived, especially where

the formation has not been completed. We can now readily account for the impression of a small tube sometimes observed as imprinted on a larger one; the black lines running between the dots, and separating their rows, are also readily explained. In making careful transverse and oblique sections of stems of the above-mentioned plants, we can readily perceive the appearances (in Plate IV. fig. 5 of Dr. Griffith, where *a* represents the rows of dots corresponding to the projecting portion of the cell opposed to the forming tube.) The bent appearance of the fibre within the tube gives the prismatic or angular appearance to many of these tubes, so readily perceived when two vessels press against each other. In some few cases a large number of very small cells appear to act in compressing as a single large one. When I first noticed the transitions above described, I imagined they were confined to the Ferns only, but I have since found them applicable to all the plants above enumerated. A very common cause of the beaded appearance on the margins of the tubes viewed under the microscope is their longitudinal section, so that the projecting extremities of the cut fibres produce the peculiar appearance of beads." These remarks are illustrated by figures in the work referred to. It is to be regretted that the loose manner in which the word "dots" is used should cause some obscurity in the author's meaning.

Sect. V.—*Of Laticiferous Tissue, or Cinenchym.*

The earlier anatomists were acquainted with the existence of milk vessels in many plants, but they gave no account of them sufficiently exact to distinguish them from other kinds of tissue, and, accordingly, they have been usually looked upon as forms of Pleurenchym, or of Trachenchym, or as intercellular cavities.

It was reserved for Prof. Schultz of Berlin to show the general existence of such vessels, and their real nature, and upon his and my own observations, the following account of them is founded.

Laticiferous tissue (*Vital vessels, Vasa opophora*) consists of branched anastomosing tubes, lying in no definite position

with regard to other tissue, large and thick-sided when old, but so capillary and thin when young as hardly to be visible. The sides are not parallel as in other vessels, but often contracted and expanded at intervals, so that they may be described as partially closed up by strictures here and there: they are said to have a power of contraction, but there are no valves or dissepiments in their interior. The larger trunks Schultz calls *vasa expansa*, and the finer ramifications *vasa contracta*.

This kind of tissue has generally an undulatory direction. (Plate II. fig. 19). In its interior there is a quantity of granular matter, which sometimes fills it wholly, and sometimes is separated by empty spaces. Its average size is $\frac{1}{1400}$ of an inch. The sides, although they thicken by the successive deposit of new matter, never offer any marks, or pits, or other interruptions of continuity.

It is obvious from these characters that cinenchym is different from every other form of tissue. Its constant, irregular branching and anastomosing would alone distinguish it.

As such vessels lie in no definite direction with respect to the rest of the tissue, they have been generally overlooked, and are often very difficult to find, although always present in the greater part of flowering plants. M. Schultz recommends maceration for five or six days, as affording a ready means of separating them from the surrounding tissue; and I quite concur with him in this recommendation. It is, however, easy to find them in the liber of the Fig, in the roots of Dandelion, Scorzonera, Lettuce, and other milky Composites, or in any of the parts of Chelidonium.

They are placed in great abundance in the innermost layers of the liber, across the Parenchym of foliaceous organs, in the bark of the root, in the pith, and probably in all other parts; but their station seems to vary in different species. Sometimes they accompany the spiral vessels, forming a part of the bundle of tissue to which those organs belong. From the interior parts they proceed by finer and finer ramifications.

In the lowest orders of plants, and in some others, they are

wholly wanting. They are largest in plants having milky juice, and smallest in those whose juice is transparent.

Plate II. contains representations of several laticiferous vessels. Fig. 16. shows them thin-sided and filled with latex. Fig. 17. represents them thick-sided and filled with latex. Fig. 19. shows them empty. At fig. 12. *a*, and *g*, they are seen parallel with the other tissue, filled with latex, and a little contracted at intervals.

The analogy between laticiferous tissue, and the other forms, is not well made out. Schleiden declares that he is not quite satisfied as to its cellular origin, and regards that question as being uncertain. He describes cinenchym thus: "It resembles large intercellular passages; no proper membrane is visible, but it may be so thin as to escape our observation. What is very remarkable however is, that at the juncture of two adjacent cells, where there must be an intercellular passage, as in all true cells, there should still be no membrane visible; in old isolated vessels, depressions and sharp angles are clearly visible, whence it is clear that the vessels must have been closely pressed by the surrounding cells. The vessels are generally so numerous and anastomose so much, that it is hardly possible to trace them along their whole course; this may, however, be done by dissolving the surrounding tissue in nitric acid. Without such a contrivance, they can generally be seen to stretch across the whole of a part of a plant, but then they often terminate abruptly, especially in the side branches; this is remarkably evident in leafless Euphorbias, and one cannot help wondering how there can be any dispute about the matter. On the sides of old vessels, especially in the stems of leafless Euphorbias, spiral streaks and layer-like thickenings can be seen, so that the gradual development of these formations agrees entirely, thus far, with that of cells." (*Grundzüge*, 2nd edit. p. 254.)

Mr. Henfrey regards it as "intercellular passages which become lined by a proper membrane:" but such appearances as are represented at Plate II. fig. 19, seem to be irreconcilable with his hypothesis.

I believe the laticiferous tubes to be strings of cells united at their ends, and with the partitions absorbed. The common

Plantain (Musa paradisiaca) seems to prove this to be so. In this plant there occurs a beautiful form of tissue, which, when young, consists of strings of transparent cells, resembling beads, each with a large cytoblast; at a later period these beads are so blended, that they form long continuous uninterrupted lines, referable to Schultz's *vasa expansa*, and very like the tissue figured by Schleiden (p. 252, f. 61), from Bifrenaria atropurpurea; at that time they are of a deep brown colour; but with age, or under the action of boiling potash, they separate into short fragments evidently representing original cells. This tissue deserves to be very carefully studied.

SECT. VI.—*Of spurious elementary Organs; such as Air Cells, Receptacles of Secretion, Glands, &c. &c.*

The kinds of tissue now enumerated are all that have as yet been discovered in the fabric of a plant. There are, however, some other internal parts, which although not elementary, being themselves made up of some one or other of the forms of tissue already described, nevertheless have either been sometimes considered as elementary, or at least are not referable to the appendages of the axis, and can be treated of more conveniently in this place than elsewhere. These are, 1. *Intercellular passages;* 2. *Receptacles of secretion;* 3. *Air cells;* 4. *Raphides.*

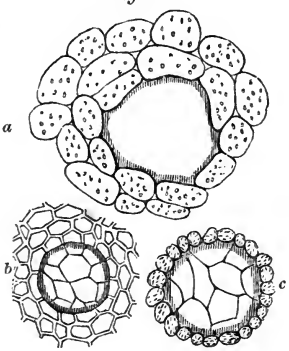
1. Of Intercellular Passages.

As the elementary organs are all modifications of either the spherical or cylindrical figure, it must necessarily happen that, when they are pressed together, spaces between them will remain, which will be more or less considerable in proportion as the tissue preserves in a greater or less degree the cylindrical or spherical form. When the pressure has been very uniform, as in the case of the tissue of the epidermis, and in other states of cellular substance, or when elementary mucus holds the tissue together completely, no spaces will exist. When they do exist, they are called *Intercellular passages.* They necessarily follow the course of the tissue, being hori-

zontal, vertical, or oblique, according to the direction of the angles of the tissue by which they are formed. Their size varies according to the size of the tissue and the quantity of sap. In plants of a dry nature, they are frequently so small as to be scarcely discoverable; while in succulent plants they are so large as to approach the size of cells, as in the stem of Tropæolum majus. They are remarkably large in the horizontal partitions which separate the air cells of water plants. In Limnocharis Plumieri they exist in the form of little holes at every angle of the hexagons of which the partitions in that plant consist; and are, no doubt, there intended as a beautiful contrivance to enable air to pass freely from one cavity to another.

2. Of Receptacles of Secretion.

Fig. 10.



But it frequently occurs that the simple intercellular passages are dilated by the secretions they receive, and either increase unusually in size, or rupture the coats of the neighbouring tissue; by which means cavities are formed, filled with sap altered to the state which is peculiar to the particular species of tree producing it. Cavities of this nature are often called *vasa propria*. To this class also are to be referred the *turpentine vessels* of Grew;* the *réservoirs accidentels* of De Candolle; and also the *réservoirs en cæcum* of the latter,

* The reader may learn from Grew's words on this subject, how accurate his ideas were upon such points of Vegetable Anatomy as the microscopes of his day enabled him to study. In his *Anatomy of Plants*, p. 110, Book III., he speaks

which are the clavate vessels of oil found in the coat of the fruit of Umbellifers, and which are commonly called *vittæ*. Although the receptacles of secretion have no proper coat, yet they are so surrounded by cellular tissue, that a lining or wall is formed, of perfect regularity and symmetry. The tissue of this lining is generally much smaller than that of the neighbouring parts. When filled with a fluid having a different refractive power from that of the surrounding parts, these receptacles give a semitransparent dotted appearance to the organs in which they occur, as may be seen by holding up the leaf of an orange tree against the light.

While, however, many kinds of receptacles of secretion are mere cavities in the tissue, others are little nuclei of cells, as in the Dictamnus (*fig.* 10. *c.*) These are of the nature of glands, and are called internal glands by Meyen.

Numerous modifications of these parts have been described by German anatomists, especially by the last-mentioned author, but they only relate to the refinements of the subject. In figure, the receptacles are extremely variable, most commonly round, as in the leaves of the Orange and of all Myrtleblooms

thus of the Turpentine Vessels, or *Gum Vessels*, and what he called *Lymphœducts*, or woody tissue of the liber: —

"Those in the Barque of Pine are likewise of two kinds. The inmost are Lymphæducts, as in the two former. The utmost are not Milk-Vessels, but Gum-Vessels, or Resiniferous; which stand straggling, and singly, about the middle of the Barque. Out of these vessels all the clear turpentine, that drops from the tree, doth issue.

"Few, but very great. So that besides the difference of their Number and Position, and of the Liquors which they contain, and Bleed; there is yet a fourth, and that is, their size. Most of these Turpentine Vessels being of so wide a bore, as to be apparent to the naked eye, and through a good glass above $\frac{1}{3}$ of an inch in diameter. Whereas that of the Lymphæducts can hardly be discovered by the best microscope.

"The same Turpentine Vessels of Pine are likewise remarkably bigger, not only than the Lymphæducts, but many times than the Milk-Vessels themselves: as those of the Fig, which, in comparison, are exceeding small; every Arch, not being a single Vessel, but a Parcel or Cluster of Vessels; whereas one single Gum-Vessel in Pine is sometimes as big as two whole Arched Clusters, that is, as some scores of the Milk-Vessels in a Fig-Tree. And the said Gum-Vessels of Pine, being compared with the Lymphæducts of the same tree, one Gum-Vessel by a moderate estimate, may be reckoned three or four hundred times wider than a Lymphæduct. The like prodigious difference may be observed in the size of the several kinds of vessels of many other plants."

(Myrtaceæ), where they are called *crypts*, or *glandulæ impressæ*, or *réservoirs vésiculaires*, or *glandes vésiculaires*, or *receptacles of oil*. In Pistacia Terebinthus the receptacles are tubular; in Conifers they are very irregular in figure, and even position, chiefly forming large hollow cylindrical spaces in the bark. Those in the rind of the orange and lemon are little oblong or spherical cysts; their construction, which is easily examined, gives an accurate idea of that of all the rest.

These receptacles are most common below the surface of plants; but they often occur in wood. In Labisia pothöina the tissue is filled in all directions with little tubes, or passages containing a brown substance of unknown nature; and what is curious, they extend even into the pith, although they miss the wood.

3. Of Air Cells.

Besides the common intercellular passages, and the receptacles just described, there is another and a very remarkable sort of cavity among the tissue of plants. This is the *air cell;* the *lacuna* of Link. Like the receptacles of secretion, the air cells have no proper wall of their own, but are built up of tissue; and this sometimes takes place with a wonderful degree of uniformity and beauty. Each cell is often constructed so exactly like its neighbour, that it is impossible to regard it as a mere accidental distension of the tissue: on the contrary, air cells are, in those plants to the existence of which they are necessary, evidently formed upon a plan which is uniform in the species, and which has been wisely contrived by Providence in the manner best adapted to the purpose for which they are destined.

They differ from receptacles of secretion in containing air only, and not the proper juice of the plant; a peculiarity which is provided for by a curious contrivance of Nature. In receptacles, the orifices of the intercellular passages through which the fluid that is to be deposited drains, are all open; but, to prevent any discharge of fluid into the air cells, the orifices of all the intercellular passages that would otherwise open into them are closed up, except in the partitions that divide them from each other.

Air cells are very variable in size, figure, and arrangement. In the stem of the Rush (Juncus articulatus), they consist of a number of tubular cavities placed one above the other, and separated by membranous partitions composed of a combination of minute cells; in some aquatic plants they are very small, as in Butomus umbellatus. In form they are either cylindrical, or they assume the figure of the cells by which they are formed, as in Limnocharis Plumieri (Plate III. fig. 1. and 2), in which the structure of the air cells and their coats forms one of the most beautiful of microscopical objects. In the green parenchymatous parts of plants, such as the leaf, the cortical integument, &c., where they always abound, they are irregular spaces among the tissue, communicating freely with each other. Such as these are represented in Plate I. fig. 2.

The inner surface of the air cells, when those parts are essential to the life of a plant, is smooth and uniform. But in grasses, umbelliferous plants, and others whose air cells are apparently not essential, they seem to be caused by the growth of the outside of the stem being more rapid than the formation of the central cells; so that the central tissue is torn asunder into cavities of an irregular figure and surface. Kieser was the first to observe that, in many plants in which the air cells of the stem are regularly separated by partitions, the intercellular passages of the cells forming the partitions are sometimes open, so that a free communication is maintained between all the tiers of air cells.

M. S. F. Hoffmann has ascertained that processes analogous to the hairs of epidermis frequently exist in air passages. Although he found them in various species of Limnanthemum, he was unable to discover them in Villarsia. Yet in other orders they would seem to be more constant, for among the Water-lilies (Nymphæaceæ), the genus Euryale (ferox) exhibited the same kind of dotted hairs as are found in the air-cavities of the different organs of the genera Nymphæa and Nuphar.

4. Of Raphides, or Crystals.

Among the tissue are found certain needle-shaped transparent bodies, lying either singly or in bundles, and called *raphides*. They were first discovered by Rafn, who found them in the milky juice of Spurges (Euphorbiæ), afterwards they were met with by Jurine, in the leaves of the Snow-flake (Leucojum vernum,) and elsewhere; and they are now well known to all vegetable anatomists. If a common Hyacinth

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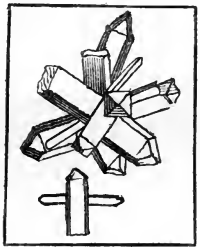

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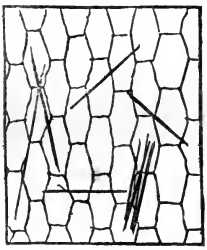

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is wounded, a considerable discharge of fluid takes place, and in this myriads of slender raphides (*fig.* 13.) are found floating; or if the skin of the leaf of the Marvel of Peru (Mirabilis Jalapa) is lifted up, little whitish spots are observable, which are composed of them; all these are acicular in form, whence their name. In Cereus peruvianus (*fig.* 11.) they are found in the inside of the bladders of cellular tissue, and, instead of being needle-shaped, have the form of extremely minute conglomerated crystals, which according to Turpin, are rectangular prisms with tetrahedral summits, some with a square, others with an oblong base. Crystals of a similar figure have been remarked by the same observer in Rheum palmatum (*fig.* 12.); and their presence, according to him, is sufficient to distinguish samples really from China and Turkey from those produced in Europe. The former abound in these crystals, the latter have hardly any. They are insoluble in alcohol, water, and caustic potash, but are dissolved by nitric acid.

Raphides are found solitary in the cells of Papyrus antiquorum, Epidendrum elongatum; &c., scattered in considerable numbers in the cells of the Plantain (Musa paradisiaca),

and collected firmly into bundles, which are a little shorter than the cells in which they lie. They are, in most instances, formed in the cells of Merenchym and Parenchym without order; but Meyen has observed that in the bark of the Wayfaring Tree (Viburnum Lantana) they are principally stationed in the interior of thin-sided cells, clustered in cavities of thicker-sided tissue.

Link compares the Raphides in plants to calculi in animals.

Raspail wrongly asserts that they are never found either in Cactus or elsewhere in the inside of the bladders of cellular tissue, but are exclusively placed in the intercellular passages. The slender kind (*fig.* 13.) he states to be crystals of phosphate of lime, from $\frac{1}{100}$ to $\frac{1}{300}$ of a millemetre in length, and to be in reality six-sided prisms, terminated at each end by a pyramid with the same base. The crystals found in the Cereus and Rhubarb (*figs.* 11. and 12.), he says are composed of oxalate of lime; and he represents them to be right-angled prisms, terminating in a four-sided pyramid. (*Nouv. Syst. de Ch. Org.* p. 522.) According to Marquart the raphides of Aloe arborescens consist of phosphoric acid combined with lime and magnesia. Right rhombic crystals are said to be carbonate of lime; octahedral crystals, and six-sided prisms, to be sulphate of lime.

Mohl says that raphides are never six-sided prisms, as Raspail asserts; but that they are right-angled four-sided prisms, which gradually vanish into points; and he declares that Meyen is right in asserting that the raphides are constantly formed inside the cells, and never in the interstitial passages of cellular tissue (*Anat. Palm.* p. 28.); about which there is now in fact no doubt. In Liparis pendula, in which the tissue is very thin, the raphides may be seen *in situ* without disturbing the surrounding parts; they there form dense bundles of acicular crystals lying in the centre of cells.

The same circumstance is particularly visible in the oval cells found in the leaves of Caladium esculentum, Dieffenbachia Seguina, and some other Arads. Here the acicular raphides are not only collected in bundles inside the cells, but are expelled from them by an opening at each end of the cell, on which account Turpin calls such cells *Biforines*.

Morren found the power of emitting their raphides preserved by these bodies after having undergone 6° of cold of Reaumur (18° Fahr.), and he therefore concludes that the phenomenon is, as Turpin supposes, a mere physical action produced by endosmose, and not a vital action.

He distinguishes from Biforines under the name of *Clestines* those well-known large cells in which Raphides, or acicular crystals, are deposited in some plants. He finds that in the Plantain (Musa paradisiaca) the clestine is produced among oval tissue of the divisions of the air-cells in the leaves of that plant, and that for a long time after the appearance of crystals in the inside, it preserves its oval figure. So long as it remains attached by a single point to the cells of this partition it retains that form, but by degrees the surrounding tissue alters into actinenchym, or starry tissue, and then its adhesion to the cells from which it receives its food takes place at several different points; whereupon in augmenting in size and gaining a much greater capacity than the surrounding actinenchym, it attaches itself to the rays of the latter by legs or peculiar extensions, which may amount to the number eight or ten. But if it is formed at the borders of the prismatical tissue of the partitions, it acquires the form of a cylinder with two beaks. He regards clestines as analogous to biforines, but differing in not possessing the apertures required for the ejaculation of their contents under the influence of endosmosis. (*Observations sur l'Anatomie des Musa, in the Bulletin de l'Ac. R. de Bruxelles,* VI. No. 3.)

In the last edition of this work, the late lamented Mr. Quekett gave the following excellent account of Raphides, which I reprint because of its intrinsic excellence, although it is in some respects a repetition of the previous observations.

General Appearance.—Raphides are most frequently observed under two forms, appearing in one instance as transparent acicular crystals, which are either distinct from each other or united into a compact fibrous bundle, and in the other instance as small bodies composed of many crystals which radiate from the same centre, thereby forming a more or less spherical mass.

Besides these two usual kinds, there are other forms, but of more rare occurrence, some of which are observed of regular crystalline figure; as the rhombohedron in some cells of Calla æthiopica, and bark of Cascarilla; octohedron, according to Meyen, in the stem of Tradescantia virginica; the rectangular prism in Quillaja saponaria; and oblique prisms, which occur with acicular crystals, in Scilla maritima: but still there are a few varieties which present an irregular crystalline figure, some of which can be observed also in Tradescantia virginica, and in the inner layers of the bark of the Lime tree, where they seem very thin and pointed at the extremities, appearing like slices cut longitudinally from the middle of a square prism, which may be imagined to possess a four-sided pyramid at each end.

Form.—With respect to the form of the *acicular Raphides*, some difference of opinion exists between Raspail and Mohl's description; the former asserting that they are six-sided prisms, terminated at each end by a pyramid with the same base; whilst the latter describes them as *right-angled* four-sided prisms, vanishing into points. It is a difficult matter to decide between these two opinions, if an entire crystal be the subject of examination; for, even if magnified 1000 times, the figure is not clearly defined: but, by having recourse to some delicate manipulation, the proper shape can be then ascertained, when it can be shown that neither of the two opinions is correct in all points.

Raspail's reason for considering the acicular crystals to be hexagonal prisms arises from the appearance they present with transmitted light, when some (but not all) are seen to exhibit two dark margins and a streak of light between them, which extends the whole length of the crystal: from this he reasons that its figure is six-sided, the lateral planes reflecting the light which impinges upon them, and consequently are seen as darkened margins, whilst the surfaces which are superior and inferior, being in a position favourable for the transmission of the rays, are transparent. This is the argument brought forward in Raspail's *Organic Chemistry*, in favour of the hexagonal figure, but there are no attempts to prove if any other form or position of an acicular crystal

could not present a similar aspect, which is the case, as will be shown hereafter.

As respects the summit being a six-sided pyramid, its existence does not seem discoverable, for the crystal from about its centre gradually vanishes to a point, having no angular interruption, such as is observed in the large crystals in the root of Iris florentina or the wood of Quillaja, where a regular right-angled prism is surmounted by a pyramid. Mohl's idea of the shape certainly approximates the truth more than Raspail's; but it can be shown, though the acicular crystals are four-sided, they are not always *right-angled* prisms, as he asserts. To witness these facts, the crystals must be obtained, by lengthened maceration, free of cellular tissue, and then crushed into fragments, when many will present an obliquely transverse fracture which exhibits four sides, some having the angles right angles, and others acute and obtuse angles; in fact, the transverse section of such would resemble frequently a rhombus. To examine more satisfactorily the fractured ends of these minute crystals, which scarcely measure the $\frac{1}{10000}$ part of an inch, it is most convenient to place their fragments in a watch glass, with a small portion of Canada balsam, and to heat the whole till the balsam has acquired a viscid consistence, then let it be removed from the source of heat, and be stirred whilst the mass is cooling till sufficiently hard, when the broken Raphides will be sustained in it in all directions; and frequently a few can be observed erect, which cannot fail to give a true outline of their real form, which by this method appears to be a four-sided prism, the angles being frequently oblique, and in other instances to put on the rectangular condition. Occasionally some of the crystals are observed to exhibit a triangular section of the isosceles shape, which seems to be an anomaly: but, to account for this, it is to be remembered that it is not opposed to the laws of crystallisation for certain bodies to crystallise in halves, consequently the half of a four-sided prism, taken from one angle to the opposite one, would be triangular; and it is conceived that when a crystal exhibits this triangular section it has belonged to the compact bundle of crystals in which it has been con-

strained to assume this form, as being fitted to fill up certain spaces better than one of the oblique or rectangular shape.

This being the observed figure, it is not difficult to account for the black margins observed in certain crystals, which may be occasioned by a rectangular prism resting obliquely, or by an oblique or triangular prism, as well as by the hexagonal; for, as the sides of either are not in the plane of direction of transmitted light, the rays are reflected, and that portion which reflects the light appears dark.

Besides these methods of determining the form of acicular raphides, if a little alcohol be added to water containing them, and examined immediately after by the microscope, the crystals can be often seen to roll over and over, and some of them will, whilst revolving, present alternately a pointed and then a flat extremity, just as if a wedge were revolving on its axis; showing that such crystals are four-sided, but two of the sides only attenuated to form the pointed appearance, the other two suffering no diminution of their breadth at any point.

That the four-sided prism is the ultimate figure of these minute crystals is rendered more probable by the occurrence of rhombohedral and rhombic prisms without pyramids, of the same composition, in the same plant, but of much greater widths; and there can be no doubt that these latter bodies and the acicular are two modifications of crystal of the same substance. The most decided proof of their being four-sided is obtained by pressing lightly on the piece of glass which covers them, whilst examined under the microscope, when those which appear six-sided instantly appear four-sided, owing to the square crystal resting obliquely: this can be seen in the minute crystals of Squill, or in the large square ones of Quillaja saponaria.

The rounded masses, which may be termed *Conglomerate Raphides* in opposition to the acicular variety, seldom present more than the pyramid of each little crystal composing them; but in a few cases, where an opportunity is afforded of examining the prism, it can be seen to be rectangular and terminated by a four-sided pyramid.

Classes of Plants in which they are found.—No division

of the vegetable kingdom seems without greater or smaller quantities of these crystalline formations, which are found in a great number of Exogens and Endogens, and likewise in Acrogens, being visible in Ferns and Mosses, and, according to Unger, in the lowest of the Algaceæ, as Nostoc Muscorum, and Conferva crystallifera.

The frequency of occurrence of these bodies is such, that it appears that, instead of those plants containing them being exceptions, those are to be considered such which have none in their tissues.

It does not appear, from numerous observations, that the acicular and conglomerate Raphides are equally common in the several classes of Plants; but that Exogens contain perhaps the one kind as often as the other, while Endogens undoubtedly contain most often the acicular variety.

Situation.—The position of these bodies has been a subject of controversy; Raspail asserting that they are always in the intercellular passages, whilst Turpin, Meyen, and Unger maintain that they are universally in the interior of the cells, which latter opinion is easily proved to be nearly correct by a little careful dissection of any plant containing them.

Raspail's advice to see these bodies is to tear a piece of the Hyacinth stem in a drop of water placed on the stage of the microscope, when numbers of acicular crystals will be visible (this method is not likely to show them in the interior of the cells); and from measuring he finds the length of the crystal longer than the ordinary cells of the tissue; and therefore he decides from this, that they cannot be contained in the interior of the cells, while he overlooks the fact that the cell in which they are contained may be often dilated to five or six times the size of those composing the ordinary tissue of the plant. The square crystals in Quillaja saponaria appear as if loose in the plant, but they are really in a cell, which cell is applied closely to the surface, the crystal completely filling it: when muriatic acid is added the crystal is dissolved, and the cell is left visible.

The most ready method of determining that the acicular crystals are contained within the cells is, to take a piece of the bulb of Scilla maritima and macerate it until it becomes

decomposed, or to take some of the rotten portions which are frequently on its exterior; and, by examining either of these with the microscope, it will be seen that there are numbers of isolated cells which contain crystals, which cells are five or six times larger than those of the tissue which have none within them; and, what appears remarkable, the crystals seldom occupy more than a small portion of the cell though it be so dilated, and in the Squill are usually collected at one end, probably by gravitation; but in the biforines they generally completely fill a small portion of the cell, about its middle, the ends containing none whatever.

To prove the same fact as regards the conglomerate kind, let a piece of the root of Rhubarb, or a part of the frond of Zamia pungens, be boiled till the cohesion of the tissue be destroyed, when some of the separated cells will exhibit one cluster generally in each; but the containing cell is not larger than others of the same plant, and at times very little larger than the mass within it.

There are some exceptions to Raphides being found constantly in cells, notwithstanding Unger's assertion that they are exclusively found in their interior, and that the vascular bundles have none within them: for they can be observed in the interior of the vessels in the stem of the Grape vine; and loose in the anthers, mixed with the pollen, in Hemerocallis purpurea, Anigozanthus flavidus, and many other plants; and they can be observed in the air cavities of many aquatics.

The interior of the *Stem* is the most common situation in the herbaceous plants for Raphides, and it used to be considered the only locality; but the epidermis of the stem of many plants displays thousands, as that of the Tradescantias, Opuntia crassa, and others.

The *Bark* of many trees also contains them; they are readily observed in the layers of the Lime tree bark, of two kinds: also in the barks of Araucaria imbricata, Cascarilla, Cinchona, and various other plants.

Even the *Pith* is not destitute of crystals; for the Grape vine exhibits them in that situation, as does the Lime tree in the medullary rays, which are processes connected with it.

The *Leaves* of multitudes of plants contain the various kinds in great abundance; Pisonia, Hemerocallis, and Calla æthiopica furnishing the acicular, whilst Rheum palmatum and undulatum are common examples yielding the conglomerate.

The *Stipules* are not without Raphides, for those of the Grape vine show them in situ, but very small in size.

The *Sepals* of many Orchidaceæ abound with crystals, as those of Bolbophyllum fuscum and others, and especially the horny labellum of Catasetum.

The *Petals* of many plants, like the sepals, contain more or less crystalline matter, which is particularly evident in the small corolla of the Grape vine.

The *Fruit* does not so often contain them, yet the common Grape furnishes a sufficient evidence of their existence in that organ.

In the *Root* their presence can be easily discovered, especially in all Rhubarbs, varying a little in number from the locality of the specimen; most in Turkish, less in East-Indian, and least in British-grown specimens.

Number in a Cell.—The number of Raphides in any cell is subject to much variation. It is seldom that a single crystal is met with; but in the Squill, Calla æthiopica, and other examples, besides the multitude of acicular crystals, some cells which are not dilated occasionally exhibit only one minute rhombohedron, as has been observed by Unger in Papyrus antiquorum. Of the *conglomerate* kind, one cluster is the usual number in the respective cells, though in Zamia pungens two such can be at times observed within the same cell. The *acicular* Raphides are in the greatest numbers, and vary somewhat in quantity in different cells and in different plants; some containing but very few, whilst others contain hundreds.

Proportion to the weight of Tissue.—The mass of crystalline matter that is formed in the tissue of some plants is prodigious, whilst in others the quantity is very thinly diffused. In several species of Cactaceæ the crystals equal if not exceed the weight of dried tissue; this is especially the case in Cereus senilis. In Turkey rhubarb root, one hundred grains yielded between thirty-five and forty grains of Raphides; and the fact

of various rhubarbs giving different feelings of grittiness to the teeth when chewed, is said by Guibourt to be employed as the test of their goodness. In the bulb of Scilla maritima, not more than ten grains are contained in the same weight of dried tissue.

Size.—The acicular vary exceedingly in their measurement, some being not more than $\frac{1}{1000}$ part of an inch in length, whilst others will be as much as $\frac{1}{40}$. The conglomerate form is not subject to so much variation, varying only from $\frac{1}{50}$ to $\frac{1}{250}$ part of an inch. The size of the rhombohedral and other forms of crystals has no uniformity as to measurement, some being not more than $\frac{1}{2000}$, whilst others are the $\frac{1}{40}$ part of an inch.

Composition.—According to Raspail, the composition of the acicular and conglomerate forms differs, the former being phosphate, whilst the latter are oxalate of lime. Unger mentions that Buchner, Nees von Esenbeck, and others, have found that their bases are sometimes lime, magnesia, and silica, the latter not often occurring; and that these bases are united to carbonic, oxalic, and phosphoric acids. The whole of these assertions are more or less correct, but Raspail has only given us negative proofs of their composition. It is not difficult to obtain positive ones, by the following experiments:—

If Raphides of the *conglomerate* form (perfectly free from cellular tissue) be heated red hot, it will be observed that they at first become black and again white, as the heating is continued to redness: in this state they readily dissolve in weak nitric or hydrochloric acid, with effervescence; if to this solution oxalate of ammonia be added, a copious white precipitate is obtained, which indicates that the base in this case has been lime. In detecting the acid united with the lime, the proceeding is a little more complicated. For this purpose the crystals are to be dissolved in dilute nitric acid, which occurs without effervescence; to this solution nitrate of silver is to be added, when a heavy white precipitate is produced, which, when washed with distilled water to free it from any excess of acid and nitrate of silver, is to be dried; if after this a small portion be heated in the flame of a lamp it explodes, by

which it is proved that the precipitate is oxalate of silver. These results, which may be performed with certainty with conglomerate Raphides, plainly prove their composition to be *oxalate of lime.*

The *acicular* can be demonstrated to be *phosphate of lime,* by proceeding thus. If heated red hot, they do not dissolve in acids with effervescence, a fact which essentially distinguishes the composition of the two kinds. When dissolved in dilute nitric acid, if oxalate of ammonia be added, we have the characteristic precipitate of lime; if with a portion of the acid solution be mixed a little nitrate of silver, a white precipitate is not obtained, as in the last case, but one of a lemon colour, which is such as denotes the combination with silver of phosphoric acid, which must have been furnished by the acicular Raphides.

Though phosphoric and oxalic acids united with lime are found the most frequent components of these minute crystals, there can be no doubt that tartaric acid enters into their formation in certain plants, as in the fruit of the Grape, where the crystals are found of a different figure from those in the interior of the leaves or stem; and also that *magnesia* can be frequently detected combined with lime, and perhaps never forms crystals with acid, without lime entering also into their composition.

Silica, though it frequently forms an organised part of vegetables, seldom exists as crystals in their interior. In a bark from Para, which is said to be manufactured into a kind of pottery, silica exists in abundance in granular fragments, which, however, do not put on a crystalline form.

Conclusion.—It is not known what purposes these bodies fulfil in the economy of plants, but it has been conjectured, since amylaceous matters are deposited, and again appropriated for the support of the carbonaceous portion of the tissue, according to the necessities of the individual, that these crystals may be deposits to be applied towards the mineral part or skeleton of the plant, as occasion may require: but it has been found from experiments that these calcareous bodies are insoluble in vegetable acids, and the silica of course in every thing; consequently they cannot be

taken up again, are therefore unsuited to the vital exigencies of the vegetable, and probably are of no use, even mechanically, in the several tissues which contain them, because plants of many kinds do not secrete such formations: therefore, it will be nearer the truth to regard them, as Link has done, as nothing more than accidental deposits.

In all the analyses lime has been found the greatest constituent of these bodies: and since this material is so intimately associated both with animal and vegetable organisation, as not perhaps to be wanting in any individual of either kingdom, there is every reason for its being so generally the base of such crystals. Moreover, since it is the property of some vegetables to combine, out of their materials of sustenance, varied proportions of oxygen and carbon, which, when apportioned in the ratio of three of the former to two of the latter, form oxalic acid, the presence of that agent in a plant, in contact with lime, can scarcely fail in producing a crystalline substance with it. Again, as phosphoric acid is a frequent accompaniment of animal and vegetable organisation either introduced with the food, or created out of it, (it being yet a problem to solve how this and other elementary matters are produced,) it can be readily conceived why compounds with it and lime should be formed as well as with the former acid; because, as the earthy and other matters are absorbed from the moisture of the soil, they must necessarily meet with these acids when they exist, and the vitality of the plant does not prevent their forming the crystals which have been here described; still there are some curious points connected with their production. If oxalic or phosphoric acid be added to a solution of lime, instead of crystals, a pulverulent opaque precipitate is obtained, which does not happen in the interior of the plants: therefore various experiments have been devised, to discover the method of making crystals by combining the above substances. Some have been ineffectual, such as making a plant, which contains lime in its composition, absorb water with a small quantity of oxalate of ammonia dissolved in it: from the want of temperature which would create a necessity or moisture in the plant this experiment failed. A method,

however, which succeeded was, to connect a vessel containing a solution of oxalate of ammonia with one containing lime water, by means of a few fibres of cotton: this gradual introduction of one fluid to the other formed perfect crystals of oxalate of lime on the ends of the fibres which were in contact with the lime water. This having succeeded, another attempt was made to form them in the interior of the cells of such plants as did not previously possess them: some difficulty occurred in finding any one fitted for the purpose, and at last Rice-paper, as it is termed, (the concentric slice from the pith of Æschynomene and Hibiscus,) was selected as the best material for the experiment, from its admitting an examination of their formation, by becoming transparent when charged with fluid.

This substance was placed in lime water under an air pump, and the cells were soon filled with that fluid; it was then dried and submitted two or three times to the same process: by this means the cells were well charged with lime. Portions of this substance were placed in weak solutions of oxalic and phosphoric acids, and allowed to remain. On the third day, when examined, the cells in both instances contained much precipitate, together with numerous crystals; those in the oxalic acid being precisely like the conglomerate form in Rhubarb, and those in the phosphoric being rhombohedra, but none of the acicular shape were found, even after continuing the process beyond eight or ten days.

These experiments distinctly prove the origin of Raphides, which appear to be compounds that become crystallised merely by the slow admixture of their constituents, and are probably modified by gummy, amylaceous, and other matters which are contained in the juices of the plant. Their formation does not seem confined to living structures or to any particular tissues or organs of a plant; but the process may be carried on in any situation, as can be proved in the Grape vine, in which crystals can be discovered in every organ, and in the vascular as well as in the cellular tissue.

A very peculiar view of the origin of Raphides has been taken by M. Payen, who has turned his attention to certain

stalked club-shaped bodies formed by calcareous precipitates, first observed by Meyen, who called them *Gummi-Keulen*, in some species of Ficus; and which, in Ficus elastica, resemble an ancient mace, studded with points, and attached to the top of a cell by the handle. M. Payen examined them in Ficus bengalensis, nymphæifolia, elastica, Carica, and others; in Pellitory (Parietaria officinalis), where they are very large; in Urtica nivea, Forskalea tenacissima; Nettle Trees (Celtis australis, and misissipensis); in the leaves of the Black Mulberry (Morus nigra), the Paper Mulberry (Broussonetia papyrifera); the Hop (Humulus Lupulus); and Hemp (Cannabis sativa), where such concretions are situated at the base of the hairs. They generally occur in the upper side of the leaf, beneath the epidermis; occasionally, as in the Fig Tree, in the lower side; and more rarely on both sides and at the edge, as in hemp. A large leaf of Broussonetia papyrifera contained 134,000 such concretions. Payen is of opinion that they are all contained in a membranous bag. The unorganised or crystallisable insoluble substances, he states, which are found in the interior of plants, are not deposited accidentally, but are always produced in tissues specially provided for the purpose, sometimes in the form of stalked secreting organs. He even carries this opinion so far as to state explicitly, that even "raphides in their various attenuated forms are composed of a skin filled with oxalate of lime, and developed in cells, consisting of a special tissue, containing some nitrogenous substance." This view, although adopted by M. M. Adrien de Jussieu and Richard, appears to me to require further examination. Why may not the mace-formed crystals of Ficus be caused by a drip of mucus and saline matter from the apex of a cell, the stalk being mucus only?

The cause of the presence of raphides or crystals in plants is due to the action of vegetable acids, formed by the vital processes of plants, upon such bases as may exist in the tissues, whither they have been conveyed with the sap out of the soil. Whether the production of such crystals is caused by mere chemical affinity, or is a vital process, is uncertain.

Sect. VII.—*Of Amylaceous and other quasi-organic Matter contained in Tissue.*

Inside the tissue of plants, are found various kinds of particles, some of which give colour or its peculiar turbid appearance to the fluids, others their nutritive quality to particular species.

Of these some are turned blue by iodine, and are therefore regarded by chemists as composed of amylaceous matter or starch; others are rendered olive-brown by that agent, and many are dissolved by alcohol, whence they are considered of the nature of resins: all are decomposed by cold, and appear to be connected with the function of nutrition.

1. Of Starch.

This substance is so common that no plant is destitute of it, and many, like the Potato, have the cells of their tubers or other parts of the stem filled full of its granules. The rhizome of Equisetum is so crowded with them, that when the cells are wounded, the starch grains are discharged with some force, apparently by the contraction of the membrane, so that the grains appear as if in voluntary motion, as long as the emptying the tissue continues to take place. These particles are perfectly white, semitransparent, generally irregularly oblong, sometimes compound, and marked with oblique concentric circles; they are extremely variable in size, some being as fine as the smallest molecular matter in pollen, that is, not more than $\frac{1}{25000}$ of an inch in diameter, others being as much as $\frac{1}{1000}$ or $\frac{1}{750}$. They often form the centre of the grains of chlorophyll, as Mohl has shown. In the milky juice of Euphorbia, they assume the singular appearance represented at Plate II. fig. 19. *b*., looking like short cylinders enlarged at each end into a round head: double-headed granules of this kind are not as yet found elsewhere; Morren states that they vary in form in different species of Euphorbia.

Starch grains of the smallest size have a distinct motion of

rotation when suspended in water; and this motion looks as if spontaneous; for of several floating near each other, in the same medium, a part will be in active motion, while others remain inactive.

Turpin called such granules *Globuline*, and considered them the most elementary condition of vegetable tissue; an opinion adopted, with some modifications, by Raspail, who looks upon each granule as one of the elementary molecules of tissue in a state of development. This writer assigns them a point of attachment or hilum, by which they originally adhered to the parent cell: he considers that cellular tissue is produced by the development and mutual pressure of each granule, and that all the varied forms of plants may be explained by reference to this principle. (*Nouv. Syst. de Chimie Organique*, p. 83.) Morren states that these grains of fecula are the first stage of a crowd of organs, and that he can demonstrate the free spiral thread of Collomia and Salvia to be at first an amylaceous granule. This, however, does not correspond with the statements of Schleiden, to be given presently.

Some of the starch-like granules, called Globuline by Turpin, appear to have, under particular circumstances, the power of spontaneous growth, by which they multiply and increase themselves externally. This is particularly visible in the fecula of Barley; which, if observed in its original state, is found to be composed of angular, irregular bodies, some of which are of extreme minuteness, and seem to have a power of spontaneous motion in water. Shortly after germination these bodies, according to Turpin, appear to lose their substance, to become more transparent and flaccid, a circumstance which he thinks is owing to the chemical change of their starch into sugar: the bodies, however, at this time retain their property of becoming blue under the action of iodine. When this alteration has been carried far enough, the maltster stops the new chemical action by heat and dryness, and fixes the sugar, producing malt. When the amylaceous granules are placed in water of a certain temperature, rendered sweet by the dissolution of their own sugar, and exposed to the influence of the oxygen of the atmosphere,

they produce little sprouts like themselves from their sides. Turpin states that, if examined after fermentation has been going on for some hours, they will be found to have each formed several new granules exactly like the mother-granules; and he not only considers this to be the cause of the curious phenomena observable in fermentation, but regards the granules as seeds and the result of their growth as a plant, which he calls *Torula cerevisiæ*. He adds, that in the inside of each of the new granules formed during fermentation, he finds a number of still smaller granules. I have not repeated the observations of this writer further than to ascertain that the granules in fermentation do sprout; and that they have at that time lost all their starch, for iodine produces no sensible effect upon their colour; a circumstance to which he has not adverted.

The true nature of starch is a modern discovery, and has been determined with great precision by the successive observations of Raspail, Fritzsche, Payen, Mohl, Schleiden, and others. The following admirable explanation is abridged from the latter author's *Grundzüge*, 2nd edition, 1845 :—

Starch, when dry, is tolerably hard, and falls to powder when rubbed between the fingers; when moist, it is rather gelatinous; when dried from solution it at first forms a trembling jelly, and afterwards becomes vitreous, brittle, and as clear as water (even in Lichens); when perfectly clean and fresh from the plant, starch gradually dissolves in water (or only disperses? for the so-called solution cannot pass through a cellular membrane); in the plant it is usually protected from solution by an incrusting wax, albumen,* mucus, or any such substance outside. Starch is easily (partially) soluble in boiling water, acids, and alkalies; insoluble in alcohol, ether, volatile or fat oils; it is stained blue by iodine, even in dilute solutions, (and the iodide of starch is not more soluble in water than ordinary starch, but it is insoluble in acids.) It appears to be changed through intermediate matter, as for instance, Lichen starch, into *Amyloid;* through the material discovered by Henry in the mace, into mem-

* Used in the sense of Chemists, not of Vegetable Physiologists.

brane, vegetable jelly, and perhaps also into gum. The chemical composition of starch is now placed beyond doubt, by the distinguished chemists *Berzelius* and *Liebig*, and is given thus—

C	H	O
12	20	10

The following is a faithful account of my own experiments:

A. *Nature of Potato Starch.*—Potato starch, as usually purchased, forms rather a coarse, shining white powder, mixed with larger particles. It is easily rubbed fine between the fingers, and it feels hard and gritty to the teeth. When moistened, it forms bulky masses and remains so, without falling to pieces when dry. But if starch is well washed at long intervals with cold water, alcohol, and ether, it becomes an extremely fine glittering powder, which will not hold together if first moistened and then dried. Some time is required to get the starch perfectly clean, and the cleansing material for a long time shows signs of the presence of an albuminous and fatty matter.

This accounts for the conflicting opinions that have existed regarding the composition of starch; observers did not experiment upon clean starch, but upon various sorts of impure materials. Payen and Persoz first thought of thoroughly cleansing starch before use, and the result of their experiments was, that starch is a perfectly uniform vegetable product.

Under a microscope, magnifying 100 times, the single particles of starch may be seen as small, fixed, egg-shaped granules. Exceptions to this form are proportionally very rare. On the pointed end of the most perfect and distinct of those granules, fresh from the potato, a small black spot, *Fritsche's* kernel (kern), may be seen. Very rarely, and only with a much higher magnifying power, can this spot be viewed in the potato, filled with a substance so thin that it is with difficulty seen to be a hole in the solid mass. This may, however, be seen much more distinctly in starch taken from bulbs of some Lilyworts.

Around this so-called kernel, a number of lines are drawn,

sometimes white, at other times black, sometimes close together, at other times farther apart, which are at first circular, but become more and more elliptical as they inclose the kernel in their foci. The substance seen between these lines appears sometimes clear, at others dark. Single spots are often remarkably transparent, and a practised microscopical observer immediately recognises layers of various thicknesses, the outer ones being thicker than the inner, which, in fresh starch, often appear quite gelatinous. The dark lines never cut the line of the outer envelope, and, however close they are placed to each other at the narrow end, each line always runs round into itself. If a starch grain with distinct black lines is placed under a microscope, it will be seen that the lines, in whatever way they are viewed, always have the same direction. It therefore follows that these are not superficial markings, but are real layers, forming egg-shaped shells packed one over the other, and constituting the entire starch grain.

It sometimes happens that if a potato full of starch is sliced with a sharp knife, so that the grains of starch are cut through, the inner sections are full of water and more gelatinous than the outer, which are drier and more compact. Perfectly dry grains show a smaller number of lines, which, however, are often more distinct, and a broad black line resembling a small layer of air is observable. If the starch is allowed to remain in a solution of gum for a long time, the lines become less and less distinct. If it is dried with the gum, until it forms a tough mass which can be cut with a knife, a great number of sections can be obtained. In these a tolerably homogeneous substance can be seen, which has rather an irregular hole in its centre, arising from the contraction of the moist inner layer.

If starch is treated with sulphuric acid, under a microscope, various appearances are observed, sooner or later, according as the acid is stronger or weaker. After being for a short time in contact with a strong acid, that point of the grain which is touched by the acid swells into a cloudy mass and gradually dissolves. Grains of starch can often be seen, one of whose ends is dissolved, while the other is well defined and

even shows a nucleus and layers (*kern* und *schichten*). In this way the whole mass of grains may be uniformly acted upon, and so that no rupture of the outer layer, nor any discharge of the fluid contents is produced. After a longer action of the acid, two different forms of solution are observable in equal abundance, which probably depend on the acid becoming weaker. In weaker acids the grains of starch gradually become transparent and gelatinous, and swell in such a way that they at first appear depressed on one side, and, at last, after becoming cup-shaped, will be entirely dissolved at their edges. In the other form of slow action, which is probably occasioned by the concentrated acid, the so-called kernel at first becomes a visible and recognisable air-vesicle; this expands and causes one or two ragged slits in the inside of the grain, which gradually swells, becomes gelatinous, the lines disappear as far as the rent extends, and at last the whole grain becomes invisible and dissolves. The next operation of the sulphuric acid seems to be to draw water between the inner layers.

If some potato starch is just heated on a small plate, so that only a small part immediately on the plate is turned yellow, then many remarkable transitions may be observed to take place gradually, and they give under the microscope the best evidence as to the structure of the grains of starch. The first thing that happens is, of course, a drying, by which the so-called kernel is transformed into an air-bubble; this always characterises the application of a dry heat, and may always be seen in the *farinha* of Mandiocca, in Sago, &c. By degrees, as the separation of the layers takes place in consequence of drying, the separating lines become sharper, blacker, broader, and layers of air, of various breadths, become clearly perceptible: the layers are firmly attached at some points, less firmly at others, and then they readily form spaces full of air. By degrees the layers peel from one another like hollow cups, whilst an evident change into gum goes on at certain points.

If the action of water, gradually boiled, is watched, an alteration which is at first very like that of sulphuric acid, as last described, is apparent. But in the last stages the action is so far different, that the cleft in the interior becomes a large

hole, and the entire grain then looks swollen like a very thick-skinned bag. By degrees the cleft becomes less distinct, but it is evident that the pasty masses thus produced, always are traceable into a grain; and if a thin starch paste is mixed with water, and viewed under a microscope with a little iodine, the single swollen grains will be visible, whilst the additional water is not stained blue. I tried for a whole day to separate the boiled grain without success, but I think I may venture to conclude from my experiments, that starch can absorb a large (but limited) quantity of water, and can consequently swell to a great size, but that it never actually dissolves in either cold or hot water.

Lastly,—I may mention the behaviour of starch with cold water. If some starch is rubbed down with twice its volume of water for half an hour, a viscid, ropy, stiff paste will be obtained. Under a microscope a large part of the grains appears variously crushed, torn, divided, and partly pounded into small flocks, the inner (watery) layers are especially pressed out as it seems through the action of the rubbing and their combination with more water, presenting a flaky or granulated entangled mass, which may be stained blue by iodine, whilst the surrounding water remains quite colourless. All these experiments were made with purchased (impure) Potato starch, and always gave the same results. In every experiment iodine was employed, and I never observed the remotest indication of any part in the grains of starch which refused to be coloured by iodine.

From these observations it must be evident, that without the combined use of a microscope and chemical re-agents, an exact knowledge of starch cannot be hoped for.

In a growing potato, the starch gradually becomes dissolved, so that often after three months scarcely a trace of starch can be found. The grain of starch preserves its solidity to the last moment, being gradually acted upon from without inwards, and in such a way that, the ends of its principal axis making most resistance, the grain by degrees assumes the appearance of an uneven rod.

B. *On the occurrence of Starch in Plants, and its various forms.*— The useful treatise of Fritsche (*Poggend. Ann.*

Bd. xxxii.) and a few unimportant additions of *Meyen* in his Vegetable Physiology, constitute all that has as yet been published on the various forms of starch in plants. Among others the question seems to have been neglected, for, from what is set forth in some of our latest works, viz. that "starch appears in the form of small circular bodies" (Endlicher and Unger, *Elements of Botany*), it is evident that the writers have neither made observations themselves, nor read anything about the matter. The forms of starch are exceedingly various, and are often so characteristic that, as Fritsche has already observed, plants, or at least their orders and genera, may be easily determined by them. The following are the forms I am acquainted with:—

I. AMORPHOUS STARCH.—Hitherto I have found amorphous starch (as paste) only in the cells of two Phanerogamous plants, namely, in the seeds of Cardamomum minus and in the bark of Jamaica Sarsaparilla. It is probable that in the last plant heating in the fire has thus strangely changed the starch, of which there is generally an abundance in Sarsaparilla.

For the most part this paste is found in the anomalous red roots, more seldom in the yellow ones, which are not as yet distinguished in the trade as substitutes for Jamaica Sarsaparilla.

II. SIMPLE GRAINS.—In most plants the grains are solitary, clusters of two or three appearing among the others as rare exceptions.

They may be further divided thus:—

§ I.—*Roundish Grains.*

A. Central hole (Fritsche's kern), altogether wanting.

1. Very small roundish grains occur nearly everywhere in the vegetable kingdom, occasionally contained in cells, for example, in Carrots, in Cambium in the winter, in leaves as centres of Chlorophyl, &c.
2. Larger, irregular, knobby, often stunted polygonal grains, in the bulbous buds of Saxifraga granulata, in the corms of Ranunculus Ficaria.

B. Central hole small roundish.

a. with distinct layers.

3. Grains coarse, rough, and often stunted, in the pith of Cycads. Some masses resemble the grains that are met with in the scale-shaped subterranean leaves of Lathræa Squamaria. The inner layers form egg-shaped granules, as in Potato starch; the small exterior ones are comparatively irregular, being so excessively thick here and there, that the whole grain is bluntly three-cornered.
4. Grains egg-shaped. In the Potato.
5. Grains mussel-shaped. In the Bulbs of the larger Lilyworts, as in Fritillaria, Lilium.
6. Almost three-cornered in Tulips.

b. With indistinct layers, or none.

7. Grains blunt polygons in Zea mays. In albumen.
8. Grains very small sharp-cornered polygons in Oryza sativa. In albumen.

C. Central hole long.

9. Grains circular or oval, and in a dry state usually showing a star-shaped slit. In Leguminous plants, for example Pisum, Phaseolus. In seeds.

D. Grains apparently cup-shaped, with a visible hole.

10. Well marked in the rhizome of Iris florentina and in allied species.

§ II.—*Flat lenticular Grains.*

11. Layers evident or not, with a hole which may be in or out of the centre, small and round or lengthened or star-shaped and torn open. As in Triticum, Hordeum, Secale. In albumen.

§ III.—*Flat Plates.*

12. Layers visible, but it is at present doubtful whether they are really included one within the other, or are placed upon each other like watch-glasses. The first appears probable, both from analogy and from the phenomena observed in heating, and from dissolving in

sulphuric acid. Found exclusively in Gingerworts (Zingiberaceæ) in the rhizomes; not in Marants.

§ IV.—*Club-shaped Granules.*

13. With long central holes, in the milky sap of European and some tropical Spurgeworts (Euphorbiaceæ.)

§ V.—*Perfectly irregular Grains.*

14. In the milky juice of most tropical Spurgeworts.

III. COMPOUND GRAINS.—Single grains are only found as exceptions in this group.

§ I.—*Single united Grains without an apparent central hole.*

15. Two, three, or four simple grains are united in the rhizome of Maranta (West-Indian Arrowroot), in the tubercles of Aponogeton, in the thickened disjointed parts of the leaves of Marattia, and in the root of Bryonia.

16. From 2—6 grains, usually united regularly, seldom irregularly, in the bark of the roots of all sorts of Sarsaparilla.

§ II.—*Single united Grains with an apparent central hole.*

A. All parts of the grains of nearly the same size.

17. From 2—4 simple grains united, the central hole being small and round. As in the tubercles of Manihot.

18. From 2—4 simple grains united, the central hole being large and mostly torn in a stellate manner. As in the corm of Colchicum autumnale.

19. From 2—4 simple grains united, each grain being hollow and apparently cup-shaped. This remarkable form occurs in the Grass oil plant: Radix Iwarancusæ (Anatherum Iwarancusæ.)

20. From 2—12 grains firmly united in very irregular masses. In the rhizome of Arum maculatum.

21. A great number (often as many as 30) small round grains joined so as to form loose spherical masses. Frequent in the stem of Bernhardia dichotoma.

B. Small grains united round a much larger one.

22. In Sagus Rumphii, &c., in pith, mostly in sago.

Starch is the most common of all vegetable productions. I know of no plant that does not in some season or other, at least in the time when vegetation is at rest, secrete starch in more or less abundance, often only in single grains in the cells, but often also swelling the cells from the large quantity of it. The grains of starch adhere to the cell walls, for the most part accidentally, by means of mucus. The supposed hilum, by which the grains of starch have been said to be held to the sides of the cell, is one of Turpin's innumerable careless representations, and is entirely without foundation. The largest starch-grain does not appear to be more than 0·05 of a line in the longest part. Starch can generally be separated from the cellular tissue by bruising and washing with water; often, however, it cannot, as, for example, when it occurs united to mucus, as in Hedychium. Starch seems to be purest in Maranta arundinacea. It is not too much to say, that for two-thirds of mankind starch is the most important, if not exclusive, source of nourishment. It is certain that starch occurs in all plants, but not always in such a state as to suffice and become fit for food; it often cannot be separated from other disagreeable substances, as in the horse-chesnut. Certain parts of plants secrete it more than others, viz., the albumen of the seeds (Grasses), the cotyledons of the embryo (Leguminous plants), pith (Cycads and Palms*), bulbs (Lilyworts†), tubers, rhizomes and roots of several different orders.‡ In less abundance, it is found throughout the winter in the bark and sap of trees; hence the possibility of making bread from the bark of trees in polar countries.

This very detailed account does not, however, touch the important question of the source from which starch grains

* Sago from Cycas revoluta, Sagus Rumphii, farinifera, &c.

† Lilium camtchaticum used as food in Greenland.

‡ Potato, from Solanum tuberosum; Cassava, from Jatropha Manihot, Tarro from Arum esculentum, &c.

are derived. So long as a hilum or point of attachment is admitted to exist, so long the starch grains may be supposed to grow from the sides of the cells. That view is adopted by Payen; but we sometimes find crowds of starch grains in cells, filling the entire cavity, in which case the central grains cannot have any communication with the cell walls. This occurs in Maize, and is fatal to the theory of starch grains springing from cell walls.

The late Mr. Quekett has given the following description of the manner in which he believed that he had seen the starch grains form. (See *Annals of Natural History*, vol. xviii. p. 193.)

"In the very young stem of Circæa Lutetiana, or the young branch of the Grape-Vine, the different appearances presented by the grains of starch, from their perfect state down to their first commencement, may be readily observed by making numerous sections from the lowermost internode up to the terminal joint. The cells most recently formed are so filled with mucilage and granules as to be opaque; lower down the granules begin to disappear, and the cytoblast is apparent; still lower, the cytoblast appears to have lost its granular character without having much increased in size, and has become a minute cell, with a distinct nucleus, instead of a congeries of granules with a larger central one. On the outside of this nucleated cell, granules (varying in number from ten to twenty) make their appearance, at first very minute and of a green hue, and afterwards enlarging and becoming colourless; and as they increase in size the nucleated cell is absorbed, and the granules become free. At a later period a multiplication of the granules takes place by fission and pullulation, certain grains exhibiting marks of subdivision, and others having minute granules attached to them; and generally more grains of starch are found in a cell than the number of minute granules seen developing on the nucleus. Several of these stages are more readily seen in the tuber of the Potato. If a slice be removed from its exterior, so thin as only to pass beneath the cuticle, and a very thin and perfectly transparent slice be then taken and examined under the microscope, the cells in the central portion are seen to contain only a few grains of starch,

while in approaching the sides of the section the grains become smaller, and pass gradually into the nature of chlorophylle. On directing attention to those parts of the section, in which the cell-contents pass gradually from the state of starch to that of chlorophylle, many cells are seen to contain a distinct nucleated cell, apparently of a flattened or lenticular form, on the edge of which are arranged a number of minute granules; in others the appearances are more advanced, the granules gradually becoming larger, and the nucleated cell becoming obliterated. From the disturbance that takes place in the position of the granules after detachment from the nucleated cell, it is difficult to determine by what part they were adherent to it; but Mr. Quekett believed that this adherence takes place at the end at which the point or hilum is observed. Subsequent to this period the grains of starch enlarge, become laminated, and are multiplied in the manner already pointed out by various observers."

Karl Muller regards starch grains as a modification of the cytoblast, founding his opinion upon appearances observed in the nucule of Chara crinita in an early stage. He found that in this plant, after long maceration, the kernel of the nucule readily emptied itself of its cells on a little dissection with a knife. He then perceived all the progressive stages of latter cell-development, so that the formation of starch-grains could be readily examined with the aid of tincture of iodine. The result was that cytoblasts are transformed into starch; but the process occurs in mature cells only.

"If," he says, "there is only one cytoblast in a cell, and this does not contain any further *cytoblasteme*, the cytoblast becomes simply expanded in all directions until it has reached the circumference of the cell-membrane which surrounds it. It then exhibits an extremely thick dark outline, whence we may conclude that its membrane is tolerably thick. At the same time it is not perfectly homogeneous, but of a granular structure. But when the outline of the other hemisphere which lies beneath it is examined at the same time, it may be most distinctly perceived that the cytoblast is hollow. This is particularly well seen when it has been coloured very pale blue by tincture of iodine. At the same time we

generally perceive within the cytoblasts some more or less roundish, and more or less curved granules. This is the simplest case. The formation must necessarily become more complex, when in addition to the cytoblast, which is hollowed out and has become converted into starch, several other cytoblasts occur. If this happen, the membrane of the primary cell generally becomes very thick in some places, *i. e.* a granular mass has been deposited upon it, which must be considered as cytoblasteme, because its structure is of the same granular kind as that of the other parts of the Chara, (for instance the cytoblasteme between every two cells, from which new cells are formed, consequently an intercalary growth,) and is coloured yellow by iodine. In this mass some portions are heaped up, forming one or several more or less globular groups which become expanded and hollow. They are cytoblasts, which do not, however, form any solid membrane on their surface, which by its expansion might enlarge so as to form a homogeneous vesicle, as ordinarily occurs in the process of cell-formation. Thus, whilst in the latter case a thin layer of the cytoblast dilates into a homogeneous membrane, in the former the whole mass of the cytoblast is expanded, whence it must necessarily become hollow. It appears, however, as if the external lamina of the circumference of the cytoblast is always composed of a harder but still not homogeneous structure. I have often observed, that when there was only one cytoblast present in the primary cell, it was encircled by the cytoblasteme, in which it could be moved like a loose nucleus, by rolling the cell to and fro." (*Annals of Natural History*, vol. xvii. p. 73.)

The correctness of this view seems to be established by an attentive consideration of the curious structure which exists in the tubercular roots of many terrestrial Orchids, such as those which form the Salep of the shops. I have shown that such roots abound in large cells filled with a matter as clear as water, and apparently of the nature of bassorin; and that this bassorin-like principle is composed of minute cells, each with its cytoblast, so compactly aggregated in the interior of the parent cell, that from this circumstance, and from their very equal refracting power, they form an apparently homo-

geneous mass. Now if such minute cells were to acquire the chemical condition of starch and its physical properties, they would be placed quite in the same manner as the grains of that substance lie in the interior of Maize, and could not be distinguished. Upon this supposition the theory of starch would be that, 1, vegetable mucus is secreted in the interior of the cell; that, 2, cytoblasts are generated in that mucus; and that, 3, the cytoblasts, under the influence of the plastic power of vitality do not become common cells, but change their physical and chemical nature till they are finally resolved into starch grains.

The mucus of vegetation does in fact sometimes take on the chemical quality of starch without becoming organised. In other words, fluid (not granular) starch is known to occur in some plants, as has been proved by Link, who remarked it in the tubercles of Salep and of the common Orchis latifolia, both before and after flowering, as he has shown in fig. 13 of the 16th plate of his admirable Anatomical figures.

He therefore concludes that the unformed matter of starch is capable of transforming itself into grains. "A thick fluid mass," he adds, "which cannot be coloured by iodine, mixed with large granules of starch, is also found in the seed of Phaseolus vulgaris. Large and small granules of starch are generally mixed with each other. The most external cells of the grain of wheat, in which, according to Payen, the most gelatine is contained, contain small granules of starch, as if they were developed from gelatine." "The mucilage of Marsh Mallows also, at least partially, belongs to the genus Starch; it forms grains, which become blue on the application of iodine, which dissolve in cold water, and which form a mucus that is likewise turned blue by the tincture of iodine." (See *Icon. Anat. Bot., table* 16, *fig.* 14, *a. b.*)

The exact nature of the action upon starch of iodine, by which that substance has been found in all cases discoverable, has been investigated by Mohl with his usual consummate skill. It has been supposed, that starch is the only known substance which becomes blue or violet when acted upon by iodine. Mohl has, however, shown either that other substances are so acted upon, or that starch exists in other states

than that of grains, as has lately been pointed out. Schleiden had remarked, that when cells are boiled in a ley of caustic alkali till they are dry, they are stained blue by the action of iodine, but lose the property by a prolonged ebullition in water. He did not, however, absolutely admit that by this process, the lining of cells is changed into starch, but he thought it most probably was so, because when weak sulphuric acid acts upon vegetable tissue, and iodine is added, a small quantity of iodine of starch is obtained. He supposes that by this operation the primitive membrane of cells is also changed into starch. He also considered that when woody tissue is converted into gum and sugar by the action of sulphuric acid, that action is secondary, a conversion of it into starch always taking place in the first instance. Schleiden also found that the embryo of Schotia latifolia is completely soluble in water, except the epidermis, and that this solution became blue by the action of iodine; wherefore he inferred that he had found a plant whose cellular tissue is in its natural state all starch.

Mohl's object was to pursue this inquiry without calling in the aid of re-agents. When the cells of the cotyledons of Tropæolum majus are sliced thin, and acted upon by a concentrated tincture of iodine, they become a fine indigo-blue, but not suddenly; they are at first yellowish, and it is only after some time they become blue, and then it is through a transition from green, owing to the mixture of yellow and blue particles. In the meanwhile the primitive membranes remain yellow. But if such a slice is placed for a few seconds in strong caustic alkali, and is then washed in water, iodine then colours the cells at once of a clear indigo-blue, and the primitive membrane acquires the same colour, but paler. The cells of Tropæolum are horny at first, and swell up when treated with water; the same kind of texture occurs in Lichens, and Professor Mohl, in consequence, directed his observations to those plants. Although he did not meet with all the success he expected in the course of their examination, nevertheless he found that the shields of many species presented a similar phenomenon; for, in many cases, iodine produced a most beautiful indigo-blue, both in the asci,

composed of primitive membrane, and in the intercellular substance that unites the cells.

In examining the horny albumen of Endogens, several interesting remarks were made. The cells of which it is composed are generally very thick-sided, perfectly colourless, and are readily distended with water. When a slice of such albumen, previously softened in water, is exposed to the action of a concentrated tincture of iodine, the cellular membranes presently acquire colour; but it is not easy to describe in what way the changes of colour take place, because at first the iodine does not produce the colour which eventually results from its prolonged action. In general it produces at first a yellow, which, by the intense action of iodine, becomes brown; moreover this agent produces, in most cases, if it acts long enough, a blue colour. This blue is, however, never of the clear indigo tint that is observed, for instance, in the shields of Lichens, but it is always reddish, and of all tints from vinous to violet, so that, in fact, it presents all the tints observable in vapour of iodine of different degrees of density.

From these and a great many more observations, Professor Mohl draws the following conclusions:—

1. Iodine causes the cellular membrane of plants to assume different colours, according to the quantity of it that is absorbed; a small quantity produces a yellow or brown tint, a larger quantity forms violet, and a still larger amount of it causes the production of blue. Iodine may be communicated to cellular membrane in the form of vapour; but the violet or blue colours are only formed when the membrane is saturated with water. Blue changes to violet or red as the membrane dries, and returns when it is again moistened. Similar variations of colour are obtained with common starch, according as it is dry or moist.

2. The colour that the membrane of cells assumes, under the action of iodine, is not dependent merely upon the quantity of iodine employed, but is also connected with the organisation of the membrane itself. Membranes which are softest and most tenacious, distending most in water, assume, even when acted upon by only a small quantity of iodine, either a violet or blue tint immediately, or at first a yellow hue, which

passes afterwards into violet or blue, even before the evaporation of the liquid. Membranes that are harder, more brittle, and less distensible in water, on the contrary, assume, under the action of iodine, a yellow or brown colour, and do not show a trace of blue, after being dried and again moistened, unless a great quantity of iodine has acted upon them.

3. The development of a blue colour is an attribute of the cellular membrane itself, and may be caused by the absorption of a sufficient quantity of iodine.

It is for chemists, says Professor Mohl, to say whether iodine colours cellular membrane by merely interposing itself between the particles of that membrane, or whether iodine and woody fibre form determinate chemical combinations, of which one is yellow and the other blue.* Be this as it may, we cannot but regard these observations of the highest interest to all engaged in the study of Vegetable Physiology.

In connection with this subject we have a very singular phenomenon recorded by Karl Muller, as having been observed by him while examining the contents of the spore cells of Lycopodium denticulatum. "When I treated these cells with iodine, ether, and hydrochloric acid, I found that their deep indigo blue colour was changed, and they became reddish, or even wholly colourless. When I then touched the fluid in which they swam, the slight agitation instantly restored the blue colour. In a state of rest, however, this soon disappeared again, and re-appeared when the fluid was touched, and so on. But if the cells had become quite colourless, immediate contact with some object, either of metal or wood, was necessary, and then the blue colour again instantly seized upon one point—it appeared to me to be the nucleus—and extended itself over the whole cell. I have met with this remarkable phenomenon in two spores. In spite of every endeavour I

* The yellow appearance is explained upon the supposition that there exists a slight, but real modification of starch, to which the name of AMYLOID has been given. Schleiden regards it as an intermediate state between cell-membrane and starch, found in the cotyledon cells of some plants, Schotia speciosa, Tamarindus indica, &c. It is cartilaginous while dry; gelatinous when moist; soluble in boiling water, strong acids, or alkalies; insoluble in ether or alcohol. When moderately firm, it is coloured blue by iodine, losing this colour and becoming yellow by soaking in water.—(*Henfrey*).

have not hitherto been able to find it again, although I have applied an infinite variety of mixtures of the three re-agents, and also used the hydrochloric acid first and the others afterwards, or these first and that last. It is possible that a peculiar stage of the life of the cell may be here requisite, which, therefore, I have not again lighted on. I remark, however, expressly that I found this changing of colour in all the blue-coloured cells of those two cells, and consequently it cannot be attributed to any optical illusion, and the less so because I could continue this play of colour as long as I liked."

2. Of Gum and Sugar.

Under the influence of vital force starch changes into gum and sugar. *Sugar* makes its appearance as a transparent fluid, which seems as clear as water, and is not rendered turbid by alcohol, but is coloured brown by tincture of iodine, according to the greater or less degree of dilution of that agent.

Gum appears as a yellowish, more consistent, less transparent fluid, which, with tincture of iodine, coagulates into a pale-yellow colour. When vegetation has advanced to that point that gum is the latest immediate product, there appears in it a great many minute molecules, which are generally so small as to resemble dark points; at that time the fluid becomes a darker yellow upon the application of iodine. But the molecules, if they are large enough to show their colour, become dark-brown yellow. It is this mass, so transparent that it can hardly be seen till it is coloured, in which, in all cases, organisation commences, and from which the youngest structure is constituted. It may be called Vegetable Jelly, and is probably nearly the same as Pecten, the base of Gum Tragacanth, and many other kinds of vegetable mucus. It is this jelly, which, by a further chemical alteration, becomes the membrane of cells, and is afterwards the material by which they are thickened.

Vegetable mucilage of the chemist in part (Bassorine; Salep) is a horny or cartilaginous substance, when dry; when moist, it swells up in a gelatinous manner, and becomes

gradually diffused throughout cold water. It is transparent and soluble in hot and cold (?) water; in caustic alkali is perhaps converted into an acid. It is not affected by alcohol, ether, fatty or essential oils, and is not coloured by iodine. On one side it passes by various modifications into cellulose (ex. gr. the cell walls of Fucoids), and amyloid (ex. gr. some kinds of horny albumen); on the other into amylum (ex. gr. the mucilage of the Orchis tubers), and often further into gum and dextrine. Probably Pectine and its compounds are closely related here. (*Henfrey.*)

3. Of Chlorophyll.

To this is referred all the kinds of coloured granules which occupy the interior of vegetable tissue. They have a spheroidal, irregular figure, are often rather angular, and consist of a semi-fluid gelatinous substance, which seems to be a coagulum of the fluid contents of the cells. The colour of plants, especially the green colour, is produced by the presence of chlorophyll, which may be considered a vital secretion. It will be mentioned more particularly in Book II., in the chapter upon colour.

According to Nägeli, "the formation of chlorophyll takes place in the leaves, and indeed always, after the formation of starch. It seems to be produced in a similar manner to the latter. In the parts of the leaf, which gradually become green, we find within the cells, in addition to the starch grains (which originate earlier), utricles in which a more greenish matter is to be perceived, others containing three or more green granules; lastly, free chlorophyll granules separate or adhering in clusters of from four to eight. Lower down in the leaf occur only free chlorophyll granules in company with starch grains. As the parent-cells of the chlorophyll are only half the size of the starch, the investigation is difficult, and conclusions are only possible from analogy. I, however, believe myself entitled to assume that the chlorophyll granules in Caulerpa originate, several together, in separate mucilage-cells, which are afterwards absorbed." (*Annals of Natural History,* xvii.186). According

to Link, a power of motion exists in the grains of chlorophyll until a grain of starch is formed within them, when the motion immediately ceases.

Of *Chromule*, which is the fluid colouring matter of plants, nothing is known that requires to be mentioned, unless it be that it principally occurs in organs of short duration, such as petals, and that it is, perhaps, never green. "The red fluids rendered blue by alkalies, and the blue reddened by acids, all contain nitrogen, according to Liebig, but not as a base." (*Henfrey.*)

CHAPTER II.

OF THE COMPOUND ORGANS IN FLOWERING PLANTS.

HAVING thus explained the more important circumstances connected with modifications in the elementary organs of vegetation, the next subject of inquiry must be the manner in which they are combined into those masses which constitute the external or compound organs, or in other words the parts which present themselves to us under the form of roots, stems, leaves, flowers, and fruit, and which constitute the apparatus performing all the actions of vegetable life. In doing this, I shall limit myself in the first place to Flowering Plants (*Vegetable Kingdom*, p. 4.); reserving for the subject of a separate chapter some explanation of the compound organs of Flowerless Plants (*ibid.*), which differ so much in structure from all others, as to require in most cases a special and distinct notice.

SECT. I.—*Of the Cuticle and its Appendages.*

1. Of the Epidermis.

VEGETABLES, like animals, are covered externally by a thin membrane or *epidermis*, which usually adheres firmly to the cellular substance beneath it. To the naked eye it appears like a transparent homogeneous skin, but under the microscope it is found to be traversed in various directions by lines, which, by constantly anastomosing, give it a reticulated character. In some of the lower tribes of plants, consisting entirely of cellular tissue, it is not distinguishable, but in others it is to be found upon every part exposed to the air, except the stigma and the spongelets of the roots. It is, however, as constantly absent from the surface of parts which live under water. Its usual character is that of a

delicate membrane, but in some plants it is so hard as almost to resist the blade of a knife, as in the pseudo-bulbs of certain Orchideous plants. The most usual form of its reticulations is the hexagonal (Plate III. fig. 11.): sometimes they are exceedingly uncertain in figure; often prismatical; and not unfrequently bounded by sinuous lines, so irregular in their direction as to give the meshes no determinate figure (*fig.* 5.)

Botanists were formerly not agreed upon the exact nature of this epidermis; while some inclined to the opinion that it is an external layer of cellular tissue in a compressed state; others, among whom were included both Kieser and Amici, considered it a membrane of a peculiar nature, traversed by veins, or lymphatic vessels.

By the latter it was contended, that the sinuous direction of the lines in many kinds of epidermis is incompatible with the idea of anything formed by adhesions of cellular tissue: that when it is once removed, the subjacent tissue dies, and does not become epidermis in its turn, and that it may often be torn off readily without laceration.

On the other hand, it was replied, that the reticulations of the epidermis are mostly of some figure analogous to that of cellular tissue, and that the sinuous meshes themselves are not so different as to be incompatible with the idea of a membrane formed of adhering bladders. We are accustomed to see so much variety in the mere form of all parts of plants, that an anomalous configuration in cellular tissue should not surprise us. The lines, or supposed lymphatic vessels, are nothing more than the united sides of the cells, and are altogether the same as are presented to the eye by any section of a mass of cellular substance. It is certain that the epidermis cannot be removed without lacerating the subjacent tissue, with however much facility it may be sometimes separable: on the under surface of the leaf of the Box, for instance, there has plainly been some tearing of the tissue, before the epidermis acquired the loose state in which it is finally found.

There is now no anatomist who doubts the fact of epidermis being composed of cellular tissue. In many plants the cellular state is distinctly visible upon a section (Plate I.

fig. 2. *a*.); it even consists occasionally of several layers of vesicles, as in the Oleander, Cacti, and many Orchids, and it varies in the density, form, and arrangement of its component cells in different species according to the peculiar conditions to which they are exposed in the places that naturally produce them.

External to the epidermis is a thin homogeneous membrane, formed of organic mucus (see page 7) and overlying every part except the stomates and the stigmatic tissue. It was first observed by Adolphe Brongniart in the Cabbage-leaf, afterwards by Henslow in Digitalis, and by myself in Dionæa; it has subsequently been the subject of more extended observations, and appears to be a universal coating, which is even drawn over the hairs, as if to protect the tender cell forming their interior. I have found this *cuticular membrane* on the delicate petals of Hydrotænia Meleagris, from which it may be easily removed after maceration for a few days in spirit of wine; and Ad. Brongniart succeeded in separating it from the leaves of Potamogoton lucens, after very long maceration in water. It is stated to be sometimes covered with a minute granular appearance, the nature of which is unknown, and which is not found at the lines indicating the place where the cuticle was pressed upon the united sides of cells. There are some good observations upon this subject by M. Adolphe Brongniart (*Ann. des Sc.* 2 *ser.* 1. 65.), who however imagines that the cuticle overlies the stigma in Nymphæa and Mirabilis. It certainly does not cover the stomates, nor such glands as those found on the surface of the inside of the pitchers of Nepenthes.

Mohl regards it, with reason, as a secretion of the epidermic cells, whose walls become thickened next the surface by the deposit of internal layers, as happens in other cellular tissues. In proof of this he observes, that when a transverse section of epidermis is treated with iodine, the walls of the epidermic cells, in most cases, remain uncoloured; and only in particular cases, as in Hakea pachyphylla, assume a yellow tinge. But, on the other hand, in all cases a thicker or thinner layer, lying on the surface of the epidermis, becomes stained by iodine of a deep yellow or brown. In the epidermis of the

stem of Kleinia neriifolia, and in Hoya carnosa, the internal unstained layer is absent, and the external, dense, iodine-stained membrane is readily perceived to be composed of several superimposed layers, which are deposited on the external walls of the cells, within the cavity, by which means the continuation of the lateral walls of the epidermis extends to the outer surface, like an uninterrupted membrane. The same phenomenon occurs in the leaves of Hakea pachyphylla, in which this inner layer is indeed present, but which takes the stain of iodine like the proper cuticle, and proves itself by its dots to be a secondary substance when the epidermis is treated with sulphuric acid, whilst at the same time a distinct lamination can be traced in the matter deposited in the interior of the cells. Hartig ascribes a very complicated structure to the cuticle, separating it into three different layers: 1. An external membrane or *epichroa;* 2. An internal membrane or *endochroa;* and 3. A central mass situated between these membranes, and called the *mesocolla.* He says that the external membrane extends over the entire leaf, penetrates into the area in front of the stomates, and at the same time stretches over the stomate itself, while the inner membrane is immersed in the form of folds between the cells of the epidermis, and penetrates in various plants, more or less deeply into the subjacent cellular tissue, in which case it then takes its course through the intercellular passages in the form of vessels. In like manner the inner membrane is said to penetrate through the stomates, and extend into the leaves, as in Narcissus Jonquilla. I cannot find this structure. (See *Cistomes,* p. 147). And Mohl protests against its existence.

Payen has instituted an inquiry into the chemical distinctions between the Membrane of Plants, and the skin or shell of Insects and Crustacea. Link, in his abstract, thus states the result of the investigation. The chemical differences are as follow:—1st. Sulphuric acid with 1·5 atoms of water dissolves instantaneously the covering of insects, but scarcely attacks the cuticle of plants in several hours. Sulphuric acid with three atoms of water breaks up animal tissue in a few hours, whilst the epidermis of plants resists it for more than

fourteen days. 2nd. Common nitric acid with four atoms of water dissolves immediately in the cold about an equal volume of insect integument; while it leaves to vegetable epidermis for more than a month its structure and outward form. 3rd. Hydrochloric acid of twenty-one degrees, or with six atoms of water, penetrates in a few minutes the covering of insects, destroys and dissolves it, but acts very slowly on the epidermis of plants. 4th. All these solutions of animal structures, when neutralised by a soluble base, give an abundant precipitate with tannic acid; this precipitate, if washed and dried, gives ammoniacal vapours on calcination; none of these phenomena occur under the same circumstances with the membrane of plants. 5th. When an almost saturated solution of powdered chloride of lime, prepared in the cold, is brought into contact with each of these substances, and then boiled for a few seconds, it destroys and consumes rapidly the tissue of insects, whilst it acts on the epidermis of the Cereus peruvianus but slowly, and the cuticle remains longer unaffected than the subjacent cellular substance.

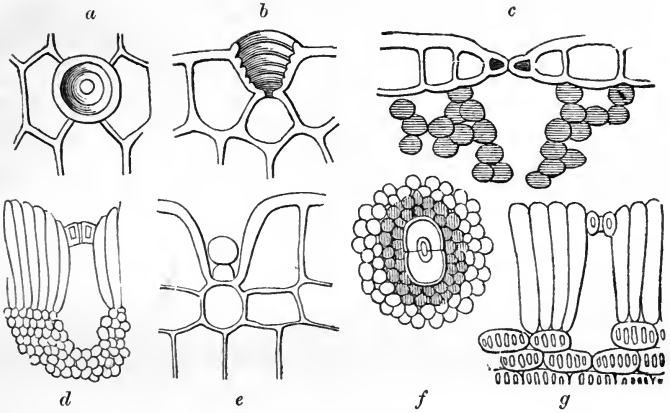
An elementary analysis gave the following results:—

Cuticle of the shell of the crab	8·935	per cent. of nitrogen.
Skin of the silkworm	9·050	„
Epidermis of potato	2·531	„
Epidermis of Cereus peruvianus (one year old)	2·059	„
„ „ (two years old)	·906	„
Cuticle of ditto	2·551	„

The greater preponderance of nitrogen in the animal kingdom is distinctly shown by these valuable researches.

2. Of Stomates.

Fig. 14.



In most plants the cuticle has certain openings of a very peculiar character, which appear connected with respiration, and which are called *Stomates, Stomata,* or *Stomatia.* (Plate III. *passim.*)

Stomates are passages through the cuticle, having the appearance of an oval or circular space, in the centre of which is a slit that opens or closes according to circumstances, and lies above a cavity in the subjacent tissue.

There is, perhaps, nothing in the structure of plants upon which more different opinions have been formed than these stomates. Malpighi and Grew, the latter of whom seems first to have figured them (t. 48., fig. 4.), call them openings or apertures, but had no exact idea of their structure. Mirbel also for a long time, considered them pores, and figured them as such; admitting, however, that he suspected the openings to be an optical deception. De Candolle entertained no doubt of their being passages through the epidermis. He says their edge has the appearance of a kind of oval sphincter, capable of opening and shutting. The membrane that surrounds this sphincter is always continuous with that which constitutes the network of the epidermis: under the latter, and in the interval between the pore and the edge of the sphincter, are often found molecules of adhesive green

matter (*Organogr.* i. 80.); and recently Adolphe Brongniart, in his beautiful figures of the anatomy of leaves, would seem to have settled the question beyond all dispute. (*Annales des Sciences,* vol. xxi.) Nevertheless there are anatomists of high reputation who entertain a directly opposite opinion; denying the existence of passages, and considering the stomates rather in the light of glands. Nees von Esenbeck and Link have denied the existence of any perforation in the stomates, and considered that the supposed opening is a space more pellucid than the surrounding tissue, and that what seems a closed up slit is the thickened border of the space. Link further added in his *Elementa* (ed. 1. p. 225.), that the obscuration of the centre of the stomates is caused by a peculiar secretion of matter, as is plainly visible in Baryosma serratum. To the views of these writers is to be added the testimony of Brown (*Suppl. prim. Prodr.* p. 1.), who describes the stomates as glands which are really almost always imperforate, with a disc formed by a membrane of greater or less opaqueness, and even occasionally coloured; at the same time he speaks of the disc being, *perhaps,* sometimes perforated. Link, however, has now abandoned his first idea (*Elementa,* ed. 2, vol. ii. p. 6.), recognising them as openings; most anatomists have come to the same conclusion, and no reasonable doubt can now be entertained that the glandular theory of Brown and others was founded on misconception.

In no plants are stomates larger than in some Monocotyledons; they are, therefore, the best subjects for examination for general purposes. In Crinum amabile they evidently consist of two kidney-shaped cells filled with green matter, lying in an area of the epidermis smaller than those that surround it, and having their incurved sides next each other. In some, at the part where the kidney-shaped cells come in contact, there is an elevated ridge, dark, as if filled with air, and having its principal diameter distinctly divided by a line. (Plate III. fig. 11.) In this state the stomate is at rest: but in others the kidney-shaped cells are much more curved; their sides are more separated from each other; and there is no elevated ridge: at their former line of contact there is an opening so distinct and wide as to be equal to half the diameter of one of the kidney-shaped cells.

This structure of the stomate in Crinum amabile may be taken as the type of all others; for, no doubt, they are all constructed upon a similar plan, though modified in different species. That is to say, they are composed of a pair of cells placed side by side, communicating freely with a hollow chamber in the parenchyma of the leaf built up of cells, arranged in various ways. (*Fig.* 14, *c* represents the appearance of the stomate in Acrostichum alcicorne when cut through perpendicularly; *figs. d* and *g* show it in the seed-coat of Canna, and *fig. f* is the appearance of the same stomate seen from above; all these are copied from Dr. Schleiden's figures.) It is not, however, always two cells which by lying side by side form the stomate; occasionally a greater number is present; as in Marchantia, where, according to Mirbel, the stomates are minute funnels in the epidermis, composed of four or five vesicles arranged circularly in several tiers; at the bottom of this funnel is a large square aperture, communicating with a subjacent chamber, and caused either by the destruction of a central vesicle, or by the separation of the sides of four or five vesicles at the angles next the centre of the funnel.

Several varieties are represented at Plate III.; besides which, stomates have been noticed by Link to be occasionally quadrangular, as in Yucca gloriosa (Plate III. fig. 10.), and Agave americana, and by Brown to be very rarely angular, of which, however, no instance is cited by that botanist. The former case is one in which the quadrangular figure is caused by the cellules of the opening being straight, and bounded by four other cells which appear to be inside the areolations of the cuticle. I have never been so fortunate as to discover the membrane which this great observer describes as generally overlying the apertures; nor do I know of any other botanist having confirmed that observation. It cannot be the cuticle already described, because it has been found that that part never overlies the stomates. (See page 134.)

Among the most remarkable forms of stomates, is that of Equisetum hiemale, thus described by Dr. Golding Bird, in the *Annals of Natural History*, vol. 18. "The fourteen longitudinal ridges on each joint of the stem are each furnished

with two parallel rows of siliceous tubercles, having the lustre and general appearance of glass beads; and along the margins of each ridge are numerous longitudinal wavy lines, which fill up the intervals between the lateral aspects of the ridges and the centres of the contiguous furrows. In the depressions of these furrows is seen a double vertical series of oval projections, arranged in pairs, each furnished with an oval fissure, having its longer axis placed transversely; these fissures lead to the complex stomatic apparatus.

Dr. Bird details the manipulations, consisting of maceration in water, boiling in strong nitric acid, careful scraping away of the disorganised cellulo-vascular structure, washing, boiling again in nitric acid, and again washing in water, which he considers necessary for the perfect exhibition of the minute structure of the stomates. After a portion of the stem has undergone these processes, the siliceous structures previously observed become much more obvious and distinctly marked. On reversing the preparation so as to obtain a view of its inner surface, the portions corresponding to the rows of tubercles are found to be nearly opaque, owing to a compact series of linear masses of siliceous matter, combined with some still remaining organic structure. Equidistant from these linear masses are seen the posterior aspects of the stomatic apparatus, each presenting an ovate nipple-like prominence having its longer axis corresponding with that of the stem, and consequently opposed to that of the external fissure, into the base of the conical eminence surrounding which these ovate bodies are fitted.

Further manipulation is necessary to carry this investigation into the more minute details, and Dr. Bird has recourse to heat, applied by holding the piece of Equisetum, prepared as already described, in the flame of a spirit-lamp, in order to get rid of the minute portion of organic matter still remaining in the preparation. After acquiring a red heat, the preparation finally assumes a snowy whiteness; it is then placed between two slips of glass, which reduce it by breaking it into fragments of a size sufficiently small to allow of careful examination by high powers of the microscope. The transverse fissure leading externally to the stomatic apparatus is found to have been widened and rendered irregular by the

heat. On bringing this fissure within the focus, it is seen to be replaced by one having its longer axis in the opposite direction, which is derived from the oval figure of the apparatus at its base. Among the fragments may be seen numerous separated specimens of the stomatic apparatus. This is described by Dr. Bird, as oval in outline, nearly flat, and measuring in its long diameter $\frac{1}{250}$ of an inch. It consists of a frame of silex formed of two pieces, thick at their convexities, thin at their concavities, nearly touching above and below, and grasping between them two long and flat structures, fissured (apparently) in a pectinate manner, and tapering from their middle towards either end. In most specimens an opening exists between these structures; in others they are quite in contact. In some the thinner and laminated portions of the frame are perforated by three well-defined apertures, but this is by no means constant. The apparatus thus consists essentially of four pieces, viz., two curved frames with their laminæ and two linear pectinated structures; and these are placed at the base of a conical eminence opening by a transverse fissure. By what means it is retained in its position, Dr. Bird has not been able satisfactorily to ascertain."

Another singular kind of stomate has been described by Dr. Joseph Hooker, in the parasite called Myzodendron punctulatum. He describes them as being placed one on the apex of each tubercle of the stem, and communicating with the cavity or chamber beneath, the respiratory cavity of some authors. "The cells of which the cuticle is composed are so completely incorporated into a uniform integument, that the curved utricles, which bound the mouth of the stoma in most plants, are here hardly apparent, though it is to their presence that the ridge is due. The aperture itself is constricted in the middle, somewhat in the form of an hour-glass, but an opening is generally, perhaps always, left between the adjacent edges of this constriction or diaphragm. The stoma thus expands both outwardly and inwardly into a sort of cup, the outer of which is frequently filled with an opaque mass, and the chambers beneath traversed by filaments of a viscid substance, stretching from one wall to the other. In the internal cavity, when empty, parallel

concentric lines may be observed, indicating the compound nature of the walls of the aperture. These stomates are abundant on all surfaces of the young stems and branches, but only on the lower surface of the older and horizontal stems." (*Flora Antarctica*, vol. i. p. 291., where it is figured. See also *Elements of Botany*, p. 21. fig. 69.)

Nerium Oleander, and some other plants have, in lieu of stomates, cavities in the cuticle, curiously filled up or protected by hairs. (See *Annales des Sciences*, xxi. 438.)

In Nepenthes there are stomates of two kinds, the one oblong, semi-transparent, and almost colourless, with numerous pellucid globules in the cavity of the cells; the other roundish, much more opaque, and coloured red. The latter do not communicate immediately with internal cavities in the parenchym, but are in contact with an internal deep brownish-red gland, the lower side of which sometimes appears to have six regular plane faces obliquely resting upon a central face, or, in other cases, to be composed of six cells surrounding a seventh, all being filled with dark red colouring matter. The nature and use of these glands, and of the stomates that accompany them, is unknown. This is I believe the only case hitherto noticed, where the same species has stomates of different forms; it is also remarkable, because in one of these cases the stomate does not open into a chamber of the parenchym, but immediately reposes upon a gland.

Although the usual condition of stomates is such as is above described, yet there are cases in which it is materially modified, and their function is changed. An instance of this occurs in Dionæa muscipula, in which the peculiar glands, placed in great numbers on the upper side of the lamina of the leaf, each proceed from a pair of parallel green cells, apparently of the same nature as the two cells forming the sphincter of a stomate.

In the epidermis of certain plants are openings resembling stomates, which require to be distinguished from them. In Nuphar luteum they occur in the form of circular depressions (*figs. a* and *b*), the sides of which are marked by elevated rings. In Peperomia pereskiæfolia (*fig. e*) they are deep impressions in the epidermis, at the bottom of which is a

two-celled hair. These have been taken for stomates by Meyen, in a plant called by him Pleurothallis ruscifolia (*Wiegman's Arch.* 1837, *t.* 10, *figs.* 4, 5, 6, 7, 8, 9); but according to Schleiden, the observations of this anatomist are incorrect, and all such appearances are either spaces left by the fall of hairs, whose bases fitted into the cavity, or formed for the reception of hairs, or depressions of an entirely different nature from stomates.

Stomates are not found in Fungals, Algals, or Lichens (see *Vegetable Kingdom,* THALLOGENS); in no submersed plants, or submersed parts of amphibious plants. They are not formed in the epidermis of plants growing in darkness, nor upon roots, nor the ribs of leaves. It frequently happens that they are found upon one surface of a leaf, but not on another, and generally in most abundance on the under side.

In succulent parts they are neither rare nor wholly wanting, as has been often asserted; but are, on the contrary, as numerous as on many other parts. They may be generally seen upon the calyx; often on the corolla; and rarely, but sometimes, upon the filaments, anthers, and styles. In fruit, they have only been noticed upon such as are membranous, and not upon the coat of the seed; not even upon those seeds which, as in Leontice thalictroides, grow exposed to air; with the exception of the genus Canna, in which Schleiden has found them, and to which he thinks them necessary in order to facilitate the passage of fluid into the interior of the seed. They exist upon the surface of cotyledons.

Their existence has been denied in Mosses; in which, however, M. Valentine has found them. Endlicher also says that Isoetes has no stomates; De Candolle figures them in that plant in his *Organographie;* and Mr. Griffith remarks that in I. capsularis they are very evident. This observer adds, that no matter, whether emerged or submerged, all plants having an epidermis have stomates.

Brown thinks that the uniformity of the stomates, in figure, position, and size, with respect to the meshes of the epidermis, is often such as to indicate the limits, and sometimes the affinities, of genera, and of their natural sections. He has shown, with his usual skill, that this is the case in Proteads,

in which statement he is supported by Schleiden, who seems to think that the structure of the stomatic opening will be modified according to the physiological peculiarities of particular species, and that it will often indicate affinity. He mentions Indian Figs (Cactaceæ,) Conifers, Pepperworts (Piperaceæ,) Agave, with some allied Lilyworts, Spiderworts (Commelinaceæ,) and Grasses, in illustration of this. (*Wiegm. Arch.* 1838. p. 59.) Brown also remarks, that on the microscopic character of the equal existence of stomates on both surfaces of the leaf depends that want of lustre which is so remarkable in the forests of New Holland. (*Journal of the Royal Geogr. Society*, i. 21.)

These views are not, however, confirmed by more extended observation. Take for example the following description given by Zuccarini of the position of stomates on Conifers:—

"In the flat leaves they usually occur only on the dorsal surface, on each side of the midrib, and form, as for instance in Abies pectinata and others, between the rib and the margin, two distinct white striæ. In Sciadopitys, on the other hand, the leaf is traversed by two parallel costæ, between which, instead of a midrib, is a strip of cellular tissue, in which the rows of stomates are situated. In Phyllocladus they are irregularly distributed between the veins, all over the under surface of the leaf; whilst in Juniperus they occur on the upper surface, in a central tract. In Thujopsis, on the contrary, and the Retinisporæ with adpressed leaves and distichous branches, and in which the under side of the leaf alone is ever visible, stomates occur on the surface of all the leaves situated on the under side of the branch. In those cases, however, in which the leaves are decussate, the under leaf of that pair which is placed above and below, is furnished with two rows of stomates, and none exist in the upper; and whilst the inferior half of each of the leaves constituting the lateral pair, which embraces the stalk, presents stomates, there are none on the superior halves of the same leaves."

Brown is of opinion, that the two glands, or rather cells, of which a stomate is composed, are each analogous to the single cells often found occupying the inner face of the meshes of the epidermis. (Plate III. fig. 9.) (See the

Memoir on the impregnation of Orchideæ.) This idea is confirmed by the structure of Yucca (Plate III. fig. 10.), in which the four oblong vesicles surrounding the stomate are evidently of the same nature as the free spheroidal vesicles (cytoblasts?) contained in the cells of the cuticle.

The following table of the proportion of stomates on the surface of various organs will serve to give some idea of their relative abundance. The first twenty-eight cases are taken from Thomson's Treatise on Vegetable Physiology, in the Library of Useful Knowledge. For the remainder I am answerable:—

	Names of the plants on the leaves of which the stomates have been counted.	Number of stomates on one inch square surface.		
		On upper side.	On under side.	On both.
1	Andromeda speciosa	None	32,000	
2	Arum Dracontium	8000	16,320	24,320
3	Alisma Plantago	12,000	6000	18,000
4	Amaryllis Josephinæ	31,500	31,500	63,000
5	Cobæa scandens	None	20,000	
6	Dianthus Caryophyllus	38,500	38,500	77,000
7	Daphne Mezereum	None	4000	
8	Epidendrum	None	4800	
9	Hypericum grandiflorum	None	47,800	
10	Hydrangea quercifolia	None	160,000	
11	Gærtnera	1000	142,750	143,750
12	Ilex	None	63,600	
13	Iris germanica	11,572	11,572	23,144
14	Olea europæa	None	57,600	
15	Pæonia	None	13,790	
16	Pittosporum Tobira	None	160,000	
17	Philadelphus coronarius	None	20,000	
18	Pyrus	None	24,000	
19	Sempervivum tectorum	10,710	6000	
20	Syringa vulgaris	None	160,000	
21	Rheum palmatum	1000	40,000	41,000
22	Rudbeckia	8000	41,000	49,000
23	Rumex acetosa	11,088	20,000	31,088
24	Theophrasta	None	172,032	
25	Tussilago Farfara	1200	12,500	13,700
26	Tradescantia	2000	2000	4000
27	Vitis vinifera	None	13,600	
28	Viscum album	200	200	400
29	Viburnum Tinus	None	90,000	
30	Prunus Laurocerasus	None	90,000	
31	Crinum amabile	20,000	20,000	40,000
32	Stapelia (stem)	.....	.....	15,000
33	Alströmeria	None	20,000	
34	Mesembryanthemum	30,000	40,000	70,000
35	Aloe	25,000	20,000	45,000
36	Yucca	40,000	40,000	80,000
37	Cereus speciosissimus (stem)	.....	.....	15,000

The origin of stomates has always been very obscure. Schleiden considers them to be the last cytoblasts which the epidermal tissue forms (see page 33 for his theory of cytoblasts). He considers that in the beginning all the forms of tissue are, in shape, contents, and structure, exactly the same, and that all the modifications of tissue take place later. He supposes that the exterior tissue of a given mass ceases to produce new cells in its interior sooner than that of the exterior, and that consequently epidermis is first completely organised; but in the epidermis some of the cells retain longer than others the property of forming internal cells, and it is when the last pair of cells separates and absorbs their parent that the stoma is produced. The cells forming the stomatic sphincter are in their origin exactly the same as the cells of the parenchym, and they remain so in their functions throughout their whole existence.

Mohl gives the following account of their origin in the Garden Hyacinth :—

"I selected these leaves," he observes (*Annales des Sciences*, 2 ser. xiii. 223) "not alone because their stomates are pretty large, but because these leaves allow, from their growing from above downwards, observations to be made on the same leaf on all the phenomena presented by the development of the stomates. Indeed, these organs are perfect in the upper and older part of the leaf, when they are not to be found at all in the lower and younger part, which is in the bulb. In the lower part of the leaves and between the cells of the epidermis, smaller quadrangular cells are seen, the transversal diameter of which is a little longer than the longitudinal diameter. These cells, as well as those of the epidermis, are colourless. Sometimes they are empty, at others they inclose a slightly granular mass.—Higher up, towards the apex of the leaf, this granular substance is found united into a globular mass, which is, however, frequently ill defined. At the same time a partition is formed in the middle of the cell and in the longitudinal direction of the leaf. This partition is at first but slightly distinguishable; but the lines which limit it soon become as visible as those which mark the sides of the cells. This partition now begins to unfold; the first trace of

a stomate is thus established, and the cell, originally simple, is divided, and forms the two cells of the pore. The cells surrounding the pore become larger in consequence of the general development of the leaf, and the intermediate slit grows at a still greater rate. The mucosogranular mass continually increases in the interior wall of these cells, and a communication is formed between it and the other sides of the cells by means of filamentous processes. Lastly, in the perfectly formed stomate the mass in the cells next the pore is equally distributed in their interior, where grains of chlorophyll are formed. The development just described proceeds very regularly in each stomate, but the same point of the leaf does not always afford stomates equally developed. Stomates are frequently found in a more advanced state than others which are close to them."

A supposed additional process of the stomates has lately been discovered beneath the epidermis, of which the following account is given by Mohl:—

"Gasparrini states, that beneath the stomates of the stem of certain Indian Thistles (Cactaceæ), in particular of Cereus peruvianus, and also of the stem of Euphorbia officinarum, and of herbaceous leaves, there is situated a vesicular organ, which he terms *Cistome*. Its walls are said to consist of delicate fibres connected by a membrane, which fibres form a sphincter at the upper end of the cistome, beneath the closed aperture of the stomate. These cistomes Gasparrini separated with the cuticle from the epidermis by boiling the latter in dilute nitric acid. Hartig, in his *Lehrbuch der Pflanzenkunde*, part. 4, 1842, describes the same organ as an appendage of the cuticle. Payen states that the cuticle enters the stomates, and in Cereus peruvianus, extends down through the layers of epidermis as a thin membrane having the form of a muff. This membrane, like the cuticle, is said to be coloured yellow by iodine, and to exhibit the same resistance to the action of sulphuric acid." In verifying these statements Mohl soaked sections of leaves in tincture of iodine, washed them with water, and then submitted them to the action of sulphuric acid. This latter agent not only heightens the yellow tint of the cuticle coloured by iodine, but it has the additional

advantage of breaking up the epidermoidal cells with the production of a blue colour, or of entirely dissolving them; after which the cuticle can be readily distinguished and separated. By this process Mohl ascertained that there is a direct continuation of the cuticle into the stomates, and thence down between the porous cells, in the form of a tube very much compressed laterally. It is certain that this tube is not closed either at the entrance into the stomates or lower down between the porous cells. At the bottom of the stomatic aperture this tube dilates into a funnel-shaped expansion, which clothes the under surface of the epidermis. The cistome differs in various plants. Generally its expanded part extends only as far as true cells of the epidermis form the outer wall of the spiracles; and it is cut off abruptly at their termination. Mohl failed to discover processes penetrating from the edge of the cistome into the intercellular passages running beneath the epidermis, and connected with the air-holes in the stem of Euphorbia officinarum, Cacalia Kleinia, Lepismium Myosurus, in the leaves of Agapanthus umbellatus, Narcissus Jonquilla, Pothos lanceolata, and in the leaf-like branches of Ruscus aculeatus. In other cases, however, he found processes evidently proceeding from the margin of the cistome through the intercellular passages on the inferior surface of the epidermis to neighbouring cistomes, thus forming communications: as on the under side of the leaves of Helleborus niger and viridis, and in the leaves of Euphorbia Caput Medusæ. In other cases, as in the leaves of Betula alba and Asphodelus luteus, that these processes penetrate into all the intercellular passages situate beneath the epidermis, and extend in the form of a net-work over the whole under surface of the epidermis, so that the epidermoidal cells are clothed on both sides by a true cuticle, which however in the inside does not form a continuous membrane.

When, says Mohl, the epidermis consists of several layers of cells, packed one over the other, as in Cereus peruvianus and in Opuntia, the continuation of the cuticle clothes the sides of that portion of the air-hole which is situated in this thickened epidermis; it appears not so much as a wide-

mouthed funnel, as a tube, and then constitutes what has been described and figured by Gasparrini under the name of a cistome. In this case the tube-like continuation of the cuticle terminates in an orifice at the bottom of the epidermis; sometimes, however, appearing to continue for a short distance into the portion of the air-hole lying between the green parenchymatous cells; as in Cereus peruvianus and Protea mellifera, which, however, has a simple epidermis. That part of the cuticle which penetrates into the interior of the leaf, is acted upon by iodine and sulphuric acid, as Payen states, precisely as the cuticle situated on the outside of the epidermis.

With respect to a fibrous structure ascribed to this apparatus by Gasparrini, Mohl observes that it can no more be demonstrated in it than in any other vegetable membrane; but as bands resembling fibres occur on the cuticle of many plants, so does the same appearance present itself in the cistomes of some plants, as, for instance, of Cereus peruvianus and Helleborus niger, &c. In like manner, as the cuticle seldom admits of our distinguishing any trace of its being made up of pieces corresponding to the subjacent epidermoidal cells, so is it with its processes lying in the interior of the leaf. They sink, indeed, into the furrows between contiguous cells, and are frequently provided at those places with projecting bands immersed in the furrows; but no composition of originally distinct pieces can be detected by the application of acids. (See *Annals of Natural History*, vol. xv. p. 217 for further details, and the *Elements of Botany*, p. 21, for figures.)

Some physiologists, Link for instance, adhere to the opinion that stomates are secreting organs, and not mere passages in the epidermis for the transmission of gaseous matter. Upon this subject I quote the words of Schleiden:—

"These two cells (of the stoma) have been designated by the name of glands, but I do not see any reason for this denomination being given to them in preference to any of the other exactly similar cells of parenchym. From these they do not differ at all in the abstract, and in their position only apparently, inasmuch as it is a law that only two cells

form an intercellular passage, not three or four; examples of which are not uncommon in the interior of plants. They contain, like the surrounding parenchym, sometimes gum, sometimes globules of mucus (schleim), sometimes starch, these latter substances sometimes colourless, and sometimes coloured by chlorophyll, but always so that their contents are the same as those of the surrounding cells: but never, as I believe, does one find in them peculiar substances which might warrant the name of glands. In the single instance of Agave lurida I remember having seen a few drops of oil. The diversity of opinions as to whether the stomates be really open, leads to the supposition, of the correctness of which any one may easily convince themselves, that their remaining open is not at all caused by a constant exterior influence, but very probably depends upon the momentary vitality of the plant, or of the organ, or perhaps only of the surrounding cellular tissue. The substances which are deposited near and upon the stomates are considered by some, with more or less plausibility, as sufficient evidence that these substances cannot be abstracted from the epidermis itself, and then they jump to the conclusion that such substances are secreted by the stomates. I have, however, in vain looked for any facts which might make it even probable, that those secretions should arise rather from the evaporation of the so-called glandular cells, than from those of the other parenchymatous cells, and more especially from such as border upon the cavities into which the stomates lead; and it appears to me that this assumed function is, in the present state of our knowledge, a mere *petitio principii*. Let us take the Conifers: here I find gum resin on the stomates; if I remove this by ethereal oil, the stomates still remain wide open; then I find a cavity (including the two cells of the stomate), and surrounded by cells which contain gum (schleim), some starch and chlorophyll, but no traces of gum resin or turpentine; on the contrary, I find, much deeper down, large turpentine vessels, and conclude now that the fluid turpentine oil escapes from these passages in the form of vapour, and following the intercellular passages, arrives in the cavities, and from here evaporates by means of the stomates into the atmosphere, by

which, as follows from its nature, it leaves behind a certain quantity of resin," &c.

Link, however, still doubts whether stomates are the air-holes of plants, and consequently the organs of respiration; he cannot find a distinct connection between the stomates and the chasms in the cellular tissue of the leaves. He cannot understand how organs of so distinct a structure should only lead to mere cavities in the cellular tissue; and the obstructing and covering matters which they produce, have always led him to consider them as organs of secretion. He however confesses that the matter is doubtful, and that he should not know what to say, if asked, "What secretions are formed by stomates in which such obstructions are not observed?"

In Nepenthes the epidermis in the inside of the pitchers is pierced by a great number of holes, each of which is closed up by a firm thick disc of small cellular tissue, deep brown in colour, and connected with the cavernous parenchym of the pitcher. Of this more will be said under the head of GLANDS.

The surface of the epidermis is either perfectly smooth, or furnished with numerous processes, consisting of cellular tissue in different states of combination, which may be arranged under the heads of *hair, scurf, glands,* and *prickles.* All these originate either directly from the epidermis, or from the cellular substance beneath it; never having any communication with the vascular or ligneous system.

3. Of Hairs.

Fig. 15.

These (*fig.* 15.) are minute, transparent, filiform, acute processes, composed of cellular tissue more or less elongated, and arranged in a single row. They are found occasionally upon every part of a plant, even in the cavities of the petiole and stem, as in Nymphæa and other aquatic plants. In the Cotton Plant (Gossypium herbaceum, &c.) they form the substance which

envelopes the seeds, and is wrought into linen; in the Cowhage (Mucuna urens and pruriens), it is they which produce the itching. In Ferns they are long, entangled, strangulated filaments. They vary extremely in length, density, rigidity, and other particulars; on which account they have received the following names:—

Down or *Pubescence* (*pubes,* adj. *pubescens*), when they form a short soft stratum, which only partially covers the cuticle, as in Geranium molle.

Hairiness (*hirsuties,* adj. *hirsutus*), when they are rather longer and more rigid, as in Galeopsis Tetrahit.

Pilosity (adj. *pilosus*), when they are long, soft, and erect, as in Daucus Carota.

Villosity (adj. *villosus*), when they are very long, very soft, erect, and straight, as in Epilobium hirsutum. *Crini* (adj. *crinitus*) are this variety in excess.

Velvet (*velumen,* adj. *velutinus*), when they are short, very dense and soft, but rather rigid, and forming a surface like velvet, as in many Lasiandras.

Tomentum (adj. *tomentosus*), when they are entangled, and close pressed to the stem, as in Geranium rotundifolium.

Ciliæ (adj. *ciliatus*), when long, and forming a fringe to the margin, like an eyelash, as in Sempervivum tectorum.

Bristles (*setæ,* adj. *setosus*), when short and stiff, as on the stems of Echium.

Stings (*stimuli,* adj. *stimulans; pili subulati* of De Candolle), when stiff and pungent, giving out an acrid juice if touched, as in the Nettle.

Glandular hairs (*pili capitati*), when they are tipped with a glandular exudation, as in Primula sinensis. These must not be confounded with stalked glands.

Hooks (*hami, unci, rostella*), when curved back at the point, as in the nuts of Myosotis Lappula.

Barbs (*glochis,* adj. *glochidatus*), if forked at the apex, both divisions of the fork being hooked, as in the nuts of the same plant.

Hairs also give the following names to the surface of any thing:—

Silky (*sericeus*), when they are long, very fine, and pressed closely to the surface, so as to present a sublucid silky appearance: *ex.* Protea argentea.

Arachnoid, when very long, and loosely entangled, so as to resemble cobweb: *ex.* Calceolaria arachnoidea.

Manicate, when interwoven into a mass that can be easily separated from the surface: *ex.* Cacalia canescens, Bupleurum giganteum.

Bearded (*barbatus*), when the hairs are long, and placed in tufts: *ex.* the lip of Chelone barbata.

Rough (*asper*), when the surface is clothed with hairs, the lower joint of which resembles a little bulb, and the upper a short rigid bristle: *ex.* Borago officinalis.

Stellate, or *starry,* when the hairs grow in tufts from the surface, and diverge a little from their centre, as in the Mallow tribe.

Hairs are either formed of a single cell of cellular tissue (Plate I. fig. 8. *b,* and Plate II. fig. 18.) or of several placed end to end in a single series, (Plate I. fig. A, B,) whence, if viewed externally, they have the appearance of being divided internally by transverse partitions. They are sometimes branched into two or three forks at the extremity, as in Alyssum, some species of Apargia, &c. Occasionally they emit little branches along their whole length: when such branches are very short, the hairs are said to be *toothed* or *toothletted,* as in the fruit of Torilis Anthriscus; when they are something longer, the hairs are called *branched,* as in the petioles of the gooseberry; if longer and finer still, the hair is *pinnate,* as in Hieracium Pilosella; if the branches are themselves pinnate, as in Hieracium undulatum, the hairs are then said to be *plumose.* It sometimes happens that little branchlets are produced on one side only of a hair, as on the leaves of Siegesbeckia orientalis, in which case the hair is called *one-sided* (*secundatus*); very rarely they appear upon the articulations of the hair, which in that case is called *ganglioneous.* (Plate 1. fig. 9. Verbascum Lychnitis): the *poils en goupillon* of De Candolle are referable to this form. Besides these, there are many other modifications: hairs are

conical, cylindrical, or moniliform, thickened slightly at the articulations (*torulose*), as in Lamium album, or much enlarged at the same point (*nodulose*), as in the calyx of Achyranthes lappacea. In Polystachya luteola the hairs of the labellum are *moniliform*, or necklace-shaped, with the articulations all spheroidal, equal sized, and disarticulating at the slightest touch when the flower is expanded, so that the part on which they grow, seems as if it were covered with fine powder.

The Rev. J. B. Reade has described a peculiar form of hair in the common Mustard. "If a seed be immersed in water, the testa, in the course of a few hours, will be covered with very minute 'vessels,' starting like radii from its surface. The peculiar refractive power of these 'vessels' renders them a remarkably difficult microscopic object. Their form is entirely novel. A number of wine-glasses, with long stems and inserted into each other, may furnish a somewhat apt illustration of their remarkable appearance; and as the walls of the bell-shaped portion are strengthened by a spiral fibre, the 'vessels' may be described in one word as fibro-campanulate."

Hairs are sometimes said to be *fixed by their middle* (Plate I. fig. 10. *c*); a remarkable structure, common to many different genera: as Capsella, Malpighia, Indigofera, &c. This expression, however, like many others commonly used in botany, conveys a false idea of the real structure of such hairs. They are in reality formed by an elevation of one cell of the epidermis above the level of the rest, and the subsequent development of a simple hair from its two opposite sides. Such would be more correctly named *divaricating* hairs. When the central cell has an unusual size, as in Malpighia, these hairs are called *poils en navette* (*pili Malpighiacei*) by De Candolle, and when the central cell is not very apparent, *poils en fausse navette* (*pili pseudo-Malpighiacei, biacuminati*), as in Indigofera, Astragalus asper, &c. In many plants the hairs grow in clusters, as in Mallowworts (Malvaceæ), and are occasionally united at their base: such are called *stellate*, and are frequently peculiar to certain natural orders. (Plate I. fig. 10. *a*.)

If highly magnified, the stellate hairs of Deutzia corymbosa

are among the most beautiful of all microscopical objects, and I can compare them to nothing so well as to stars formed of icicles covered with little glittering points. There is this remarkable in their structure, that each star has a convex centre, whence the rays diverge, appearing to be the apex of a primitive hair, of which the rays are the second joints planted perpendicularly upon it. A stellate hair of a similar kind was remarked by the late Mr. Daniel Cooper, in Croton argyræum. "The whole cuticle is closely studded with numerous very small stellate hairs (or scales), in the centre of which a small elevated circular orifice (?) is seen, probably in connexion with the stomata, and from which, as a centre, the radii proceed, giving the hair or scale a conical appearance. They may indeed be aptly compared, both as to form and apparent structure, to the inverted pappus or seed-down of a compound plant. The numerous brownish spots seen on the under surface of the leaf, are hairs of the same character and structure as those just described, but possessing this difference, viz. that the elevated orifice is of a deep chesnut colour, which tint becomes gradually diffused towards the circumference of the hair, tinging in a slight degree the radii."

Among the most curious hairs yet discovered are those on the seeds of Acanthodium, which Forskahl says, if mixed with saliva in the palm of the hand dissolve with a crackling noise (*cum fragore*). The nature of these hairs has been examined by Mr. Kippist, who has shown that the entire surface of the seed of Acanthodium is covered with whitish hairs, which adhere closely to it in the dry state, being apparently glued together at their extremities. On being placed in water, these hairs are set free, and spread out on all sides; they are then seen to be bundles of from five to twenty tubular spiral cells, which adhere firmly in their lower portions while their upper parts are free, separating from the common bundle at different heights, and expanding in all directions like plumes, forming a very beautiful microscopical object. The free portions of the cells readily unroll, exhibiting the spire formed of one, two, or occasionally three fibres, which may sometimes be seen to branch, and not unfrequently break up into rings.

Throughout the whole length of the cell the coils are nearly contiguous; in the lower part they are united by connecting fibrils, and towards the base of the adherent portion become completely reticulated. The testa is a semi-transparent membrane formed of nearly regular hexagonal cells, whose centre is occupied by an opaque mass of grumous matter. Those cells which surround the bases of the hairs are considerably elongated, and, gradually tapering into transparent tubes, appear to occupy the interior of the spiral clusters. Two species of Blepharis are mentioned as possessing a structure very similar to that of Acanthodium, differing chiefly in the smaller and more uniform diameter of the tubular spiral cells, and in their thicker fibre, which is always single and loosely coiled. The seed of Ruellia formosa on being placed in water, develops from every part of its surface single short thick tapering tubes, within which in some case a spiral fibre is loosely coiled, whilst in others the place of the spiral fibre is supplied by distant rings.

In the seeds of Ruellia littoralis, Phaylopsis glutinosa and Barleria noctiflora, the whole surface becomes covered with separate tubes, very similar in form, but destitute of spiral fibre, and terminating in a minute pore, from which streams of mucilage are discharged. (*Linn. Trans.* xix. 65.)

Very singular hooked hairs are described by the same author in the same place.

All these varieties belong to one or other of two principal kinds of hairs; viz. the Lymphatic and the Secreting. Of these, *lymphatic* hairs consist of tissue either tapering gradually from the base to the apex, or at least not much enlarged at either end; and *secreting*, of cellules visibly distended either at the apex or base into receptacles of some peculiar fluid. Malpighiaceous and glandular hairs, stings, and those which cause asperity on the surface of any thing, belong to the latter; almost all the other varieties to the former.

When hairs arise from one surface only of any of the appendages of the axis, it is almost always from the under surface; but the seed-leaves of the nettle, and the common leaves of Passerina hirsuta, are mentioned by De Candolle as exceptions to this rule: certain states of Rosa canina might

also be mentioned as exhibiting a similar instance. When a portion only of the surface of any thing is covered by hairs, that portion is uniformly the ribs or veins. According to De Candolle, hairs are not found either upon true roots, except at the moment of germination, nor upon any portion of the stem that is formed under ground, nor upon any parts that grow under water.

In a very large number of hairs, perhaps in all, there may be seen, at some period of their existence in any cell, a cytoblast, and a circulating system, formed of numerous fine streams, which all appear to proceed from and return to the cytoblast itself. (See Plate II. fig. 13. 14. 18.) In the moniliform disarticulating hairs of Polystachya, already described, each joint of the hair has this structure in a very remarkable manner.

If hairs are examined with low magnifying powers, their sides appear to be simple, and they are accordingly regarded as mere expansions or attenuations of the vesicles of the epidermis: but if they are studied with more attention and a more powerful microscope, it becomes evident that their sides are double; for currents may often be seen streaming along their sides, and evidently interposed between the external smooth surface and an uneven interior membrane. This is easily observed in the jointed hairs of Tradescantia virginica, where the nature of the current is distinctly shown by minute molecules, that are carried along by the stream. If the hair of Tradescantia is suffered to die on the field of the microscope, and dry up, it then becomes evident that it is composed of two sacs, the one firm and external, the other extremely thin, and after death contracting so much as to leave a considerable space between its sides and the external sac. (See Plate II. fig. 14. *b*.) It appears to me that this is the general structure of all hairs in which a circulation of sap, and the cytoblast are both visible; and it is probable that the external sac is the cuticular membrane, hard, firm, and scarcely capable of shrivelling; while the internal sac is protoplasm, thin-sided, and not acquiring any firmness with age, but shrivelling up as soon as the fluid which distends it when alive is withdrawn.

4. Of Scurf.

SCURF consists of thin flat membranous discs, with a ragged margin, formed of cellular tissue, springing from the epidermis. It may be considered as a modification of hairs; for it differs from those bodies only in being more compound. It is of two kinds, *Scurf*, properly so called, and *Ramenta*.

Scurfs, properly so called, are the small, roundish, flattened, particles which give a leprous appearance to the surface of certain plants, as the Elæagnus and the Pine Apple. (Plate I. fig. 10. *b*.) They consist of a thin transparent membrane, attached by its middle, and, owing to the imperfect union, towards its circumference, of the cellular tissue of which it is composed, having a lacerated irregular margin. A scale of this nature is, in Latin, called *lepis*, and a surface covered by such scales *lepidotus*—not *squamosus*, which is only applied to a surface covered with the rudiments of leaves. Scurfs are the *poils en écusson* (*pili scutati*) of De Candolle.

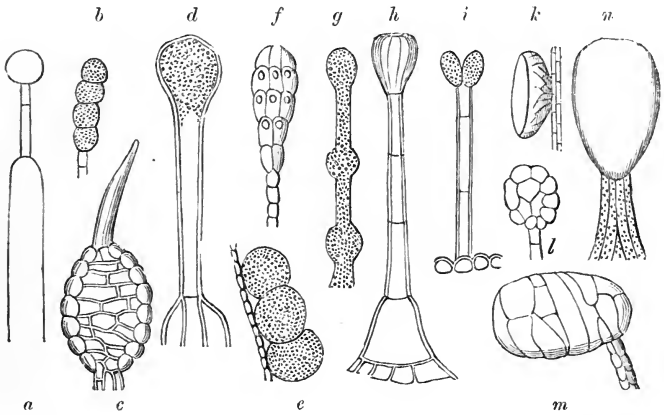
A very beautiful and peculiar form of scale has been remarked on the under surface of the leaf of "Adelia neriifolia," by Dr. Willshire, who describes it thus:— "It consists of two circular layers of cellular membrane, the one layer of much smaller diameter than the other, puckered and plaited, and of a saucer-shaped form; it is fixed by its centre, which apparently is connected with a gland having coloured contents. From this form of scale, through that met with on Elæagnus conferta, I think transitional states may be seen to the stellate hairs of many of the Euphorbiaceæ and Malvaceæ; in fact, upon the peculiar adhesions taking place between the cells depends the appearance of the stellate hairs or the scale of Adelia and Elæagnus."

Ramenta (*Vaginellæ*) are thin, brown, foliaceous scales, appearing sometimes in great abundance upon young shoots. They are particularly numerous, and highly developed, upon the petioles and the backs of the leaves of Ferns. They consist of cellular tissue alone, without any vascular cords, and are known from leaves not only by their anatomical structure, but also by their irregular position, and by the

absence of buds from their axils. The student must particularly remark this, or he will confound with them leaves having a ramentaceous appearance, such as are produced upon the young shoots of Pinus. Link remarks, that they are very similar in structure to the leaves of Mosses. The term *striga* has occasionally been applied to them (*Dec. Théor. Elém.* ed. 2. 376. *Link, Elém.* 240.); but that word was employed by Linnæus to designate any stiff bristle-like process, as the *spines* of the Cactus, the divaricating *hairs* of Malpighia, and the stiff stellated *hairs* of Hibiscus. So vague an application of the term is very properly avoided at the present day, and the substantive is rejected from modern glossology; the adjective term *strigose* is however occasionally still employed to express a surface covered with stiff hairs.

5. Of Glands.

Fig. 16.



Glands are small collections of firm cellular tissue, which is often much harder and more coloured than that which surrounds it. They are of several kinds.

Stalked glands (*fig.* 16. *a, b, c, d, f, h, i, l, m, n,*) are elevated on a stalk which is either simple or branched: they secrete some peculiar matter at their extremities, and are often confounded with the glandular hairs above described, from which

they have been well distinguished by Link. According to that botanist, they are either simple (*fig.* 16. *a, b, d, g, h, i,*) or compound (*c, f, k, l, m*); the former consisting of a single cell, and placed upon a hair acting as a simple conduit, occasionally interrupted by divisions; the latter consisting of several cells, and seated upon a stalk containing one or more conduits, formed by rows of cellular tissue. They are common upon the rose and the bramble, in which they become very rigid, and assume the nature of aculei. For the sake of distinguishing them from the latter, they have been called *setæ* by Woods and myself, but improperly; they are also the *aiguillons* of the French. In Hypericum they abound on the calyx and corolla of some species, but do not give out any exudation; they contain, however, a deep red juice within their cells. In some Jatrophas they are much branched; in many Rueworts (Rutaceæ) they form a curious humid appendage at the apex of the stamens.

The glandular apparatus of plants has received the attention of Meyen, who has published on the subject an elaborate paper, from which the foregoing figures are taken. He admits the distinction of simple and compound glands, and regards them both as unquestionable organs of secretion. To some of the former he assigns occasionally more cells than one in the gland that terminates them; but the hair to which they belong is always simple. He gives the following account of the well-known glands that clothe the leaves of the Sundew, and which have a very complicated structure; the hair exhibits in its interior a spiral tube which penetrates deep into the apex of the gland, but there is no trace of a cavity in the gland. The hairs which form the stalk of the gland are not simple excrescences of the upper walls of the epidermal cells, but true excrescences of the substance of the leaf, and appear so much more early, that the whole hair and its head may be said to be covered by the epidermis. In young organs of this kind, Meyen proceeds to say, it may be seen distinctly that the gland-head is nothing more than the apex of the compound hair which at a later period thickens. Afterwards the stalk (that is, the hair) extends to a great length, and thus the cells all acquire a lengthened form.

But with the gland-head it is different; the epidermis still retains its small cells, is generally filled with red sap, and appears to enclose red angular bodies. Directly beneath this small-celled epidermis ten or twelve large long columnar cells may be seen, which form the axis of the gland-head; when completely developed they often exhibit in their interior spiral fibres, and allow the spiral tubes of the stalk to run between them. Even in transverse sections there is nothing to be seen of a cavity in the gland-head, and that it is not present may be better seen in those glands which are found on the edges of the leaves of Drosera rotundifolia. In this species the glandular hairs are much larger than the others; the stalk is widened at the extremity like a spoon, and on the side of this spoon sits the glandular organ which effects the secretion.

On the glandular hairs of Drosera there occur here and there on the stalks other small glands consisting of two contiguous vesicular cells; these are filled with green globules, while the other cells of the stalk generally contain red sap. Dr. Willshire confirms this statement.

Of the compound glands some are hollow, others solid. They both vary exceedingly in form. The following brief descriptions of the figures at p. 159, will serve to illustrate the subject enough for an introductory work :—

Simple Glands :—*a*, a simple stalked gland, from the outside of the flower of Sinningia barbata; it consists of a cylindrical cell springing from the epidermis, then of two smaller cells, and finally of a fourth, which is the gland; *b* is a gland composed of six cells, of which the two lower are small, cylindrical, and colourless, forming a stalk, the four upper spherical, larger, and filled with secreted matter; *d*, simple pestle-shaped glands of Sisymbrium chilense; in the pestle there is a yellow volatile oil; at the base are three cells of the epidermis; *g*, from the inside of the under-lip of Antirrhinum majus: the cell containing the glandular matter is at first cylindrical; it then forms a head, from which another cylindrical joint is emitted, to which a second head is afterwards added, and upon which another joint

with its head is eventually developed; *h* is a stalked gland from the stem of the same plant; *i*, a double-headed gland from the flower stalk of Lysimachia vulgaris.

Compound Glands:—*c*, a compound sessile gland of Dictamnus albus, consisting of a skin which is colourless, and a centre which is filled with a thick green ethereal oil; *f*, compound glands from the flower stalk of Sanguisorba carnea; *k*, a side view of the compound gland of the hop, which chemists call *Lupulin* (Meyen entirely denies the accuracy of Raspail's description of this body); *l*, a compound red gland from Ailanthus glandulosa; *m*, oblong stalked glands from Begonia platanifolia: they resemble drops of resin.

Other modifications of glandular apparatus are what some Continental botanists call *papulæ*, or *papillæ* (*fig.* 16. *e* and *n*.) (the *Glandulæ utriculares* of Guettard); these are transparent elevated points of the epidermis, filled with fluid, and covering closely the whole surface upon which they appear. In other words, they are elevated, distended cells of the epidermis. The presence of papillæ upon the leaves of the ice plant gives rise to the peculiar crystalline nature of its surface.

There are, moreover, in many plants *internal glands*, that is to say, collections of cells densely compacted, and filled with secreted matter which hardens them, or renders them transparent. They are in some cases nearly of the nature of cysts, already described. In Dictamnus albus they form spherical nuclei, lying just below the cuticle, and filled with an ethereal oil, rich in resin and camphor (*fig.* 10). In Nepenthes they occur in two different states; the one as angular nuclei below one of the forms of stomate found in that plant; the other as hard, deep brown discs, lining the cavity of the pitcher, sunk below the epidermis, through which there are openings corresponding with them, and no doubt forming the apparatus by which the water contained in the pitcher is secreted. They have been noticed and figured by Meyen, but were long before mentioned in this work (1835), and have been figured by me in the second

volume of Lady's Botany (t. 47.). The opening through the cuticle immediately above them shows that they are internal organs; nevertheless, Meyen considers them external glands. Internal glands are very common in Labiates.

Sessile glands, *verrucæ*, or *warts*, are produced upon various parts, and are extremely variable in figure. In Cassias, they are seated upon the upper edge of the petiole, and are usually cylindrical or conical; in Cruciferous plants they are little roundish shining bodies, arising from just below the base of the ovary; in the leafless Acacias they are depressed, with a thickened rim, and placed on the upper edge of the phyllode; they are little kidney-shaped bodies upon the petiole of the Peach and other drupaceous plants; and they assume many more appearances. They are common upon the petiole, as in Passiflora; they are also found upon the calyx, as in some species of Campanula, and at the serratures of the leaves, when they are considered by Röper (*De Floribus Balsamineârum*, p. 15.) to be abortive ovules; and they appear upon the pericarp and the skin of the seed; in the latter case they are called *spongiolæ seminales* by De Candolle. In figure they are round, oblong, or reniform, and occasionally cupulate, when they receive the name of *glandes à godet* (*glandulæ urceolares*) from some French writers. Warts are the *glandes cellulaires* of Mirbel; but they must not be confounded with the *glandes vasculaires* of the same writer, which are not mere excrescences of the epidermis, but modifications of well known organs. (See *Discus*, further on.) Of this nature are the hypogynous glands of Cruciferous plants already referred to.

Lenticular glands (*Lenticelles* of De Candolle; *Glandes lenticulaires* of Guettard;) are brown oval spots found upon the bark of many plants, especially willows: they have been thought to indicate the points from which roots will appear if the branch be placed in circumstances favourable to their production, and are considered by De Candolle to bear the same relation to the roots that buds bear to young branches. (*Premier mém. sur les Lentic.*, in the *Ann. des Sciences*

Naturelles.) In Tree ferns it is hardly possible to doubt that the tubercles so common on the surface of the trunk, are the points of roots either prepared for development, or arrested in their growth by the dryness of the air that surrounds them; for we find (in Dicksonia arborescens, for instance) that the part of the stem which is next the ground is covered with roots, and the part above it, surrounded by drier air, is covered with tubercles. But it is not impossible that the lenticular glands of the stems of ordinary trees, and the tubercles of Tree ferns are different bodies, although so similar as to be confounded under one name.

It is extremely doubtful whether true lenticular glands are any thing more than portions of the epiphlœum, disorganised by some unknown power. Mohl states that they are found in the epiphlœum, that is, between the epidermis and the mesophlœum, and consist of greenish or colourless (or in Berberis yellow, and Sambucus red) cells which lie in rows perpendicular to the axis of the branch, and united towards the interior with the mesophlœum. He considers them a partial formation of cork.* Unger compares the true lenticular glands to the soredia of Lichens, and the reproductive granulations of Scale Mosses (Jungermanniaceæ); and he considers them in some way connected with the respiratory process: even as obliterated respiratory organs. Meyen regards them, not as obliterated respiratory organs, but as formations intended to maintain an air communication between the exterior rind and the new green bark of trees; for he says that the tissue of old bark is so compactly combined as to cut off all direct communication between the air and the cavernous parenchym of the green bark.

6. Of Prickles.

PRICKLES (*aculei*) are rigid, opaque, conical processes, formed of masses of cellular tissue, and terminating in an acute point. They may be, not improperly, considered as

* I take this from Taylor's Magazine, xii. 58, where there is an (imperfect?) translation of Meyen's report on this and other subjects. Mohl's original paper I have not seen, and the translation is in part unintelligible.

very compound hardened hairs. They have no connexion with the woody tissue, by which character they are obviously distinguished from *spines*, of which mention will be made under the head of branches; but they are a development of the epiphlœum of the bark. According to Dutrochet (*Mémoires*, i. 174), it is exclusively by the base where the epiphlœum and prickle are in contact, that the development takes place of cells to increase the prickle in size. In the Rose the prickle is formed in one year, and afterwards dies. In Xanthoxylon juglandifolium it is the produce of two or three years' growth, according to the last-mentioned author. Prickles are found upon all parts of a plant, except the stipules and stamens. They are very rarely found upon the corolla, as in Solanum Hystrix; their most usual place is upon the stem, as in Rosa, Rubus, &c.

Sect. II.—*Of the Stem, or Ascending Axis.*

When a plant first begins to grow from the seed, it is a little body called an embryo, with two opposite extremities, of which the one lengthens in the direction of the earth's centre, and the other, taking a direction exactly the contrary, extends upwards into the air. This disposition to develope in two diametrically opposite directions, sometimes called *polarity*, is found in all embryos, properly so called, there being no known exception to it; and the tendency is moreover so powerful, that, as we shall hereafter see (Book II.), the most powerful external influence is rarely sufficient to overcome it. The result of this development is the axis, or centre, round which the leaves and other appendages are arranged. That part which forces its way downwards constantly avoiding light, and withdrawing from the influence of dryness, is the *descending axis*, or the root; and that which seeks the light, always striving to expose itself to the air, and expanding itself to the utmost extent of its nature to the solar rays, is the *ascending axis*, or stem. The only exception to this is when the embryo first begins to grow. At that time the first part of the axis formed below the cotyledons belongs to the stem. As the double elongation just

mentioned occurs in all plants, it follows that all plants must necessarily have, at an early period of their existence at least, both stem and root; and that, consequently, when plants are said to be rootless, or stemless, such expressions are not to be considered physiologically correct.

The STEM has received many names; such as *caudex ascendens, caudex intermedius, culmus, stipes, truncus,* and *truncus ascendens.* It consists of bundles of vascular and woody tissue, embedded in cellular substance in various ways, and the whole enclosed within an epidermis. The manner in which these parts are arranged with respect to each other, will be explained hereafter. The more immediate subject of consideration must be those organs which are common to all stems.

1. Of its Parts.

Where the stem and root, or the ascending and descending axes diverge, there commences in many plants a difference of anatomical structure, and in all a very essential physiological dissimilarity; as will be hereafter seen. This portion of the axis is called the neck or collum, (*coarcture* of Grew, *nœud vital* of Lamarck, *limes communis,* or *fundus plantæ,* of Jungius,) and has been erroneously thought by some to be the seat of vegetable vitality. At first it is a space that we have no difficulty in distinguishing, so long as the embryo, or young plant, has not undergone any considerable change; but in process of time it is externally obliterated; so that in trees of a few years' growth its existence becomes a matter of theory, instead of being actually evident to our senses.

Immediately consequent upon the growth of a plant is the formation of leaves. The point of the stem from whence these arise is called the *node* (*geniculum,* Jungius), and the space between two nodes is called an *internode* (*merithallus,* Du Petit Thouars.) In internodes the arrangement of the vascular and woody tissue, of whatever nature it may be, of which they are composed, is nearly parallel, or, at least, experiences no horizontal interruption. At the nodes on the contrary, vessels are sent off horizontally into the leaf; the general development of the axis is momentarily arrested while this

horizontal communication is effecting, and all the tissue is more or less contracted. In many plants this contraction, although it always exists, is scarcely appreciable; but in others it takes place in so remarkable a degree as to give their stems a peculiar character; as, for instance, in the Bamboo, in which it causes diaphragms that continue to grow and harden, notwithstanding the powerfully rapid horizontal distention to which the stems of that plant are subject. In all cases, without exception, a leaf-bud or buds is formed at a node immediately above the base of the leaf; generally such a bud is either sufficiently apparent to be readily recognised by the naked eye, or, at least, it becomes apparent at some time or other; but in certain plants, as Heaths, the buds are often never discoverable; nevertheless, they always exist, in however rudimentary a state, as is proved by their occasional development under favourable or uncommon circumstances. By some writers nodes, upon which buds are obviously formed, are called *compound* or *artiphyllous;* and those in which no apparent buds are discoverable, are named *simple,* or *pleiophyllous;* they are also said to be *divided,* when they do not surround the stem, as in the apple and other alternate-leaved genera; or *entire,* when they do surround it, as in grasses and umbelliferous plants: they are further said to be *pervious,* when the pith passes through them without interruption; or *closed,* when the canal of the pith is interrupted, as if by a partition. Pervious and divided, and closed and entire nodes usually accompany each other.

Dr. Willshire thus speaks of certain supposed interruptions to continuity in the nodes of the common Miseltoe:—

"Some years ago it was stated by Dutrochet, that in the node of Viscum album no true woody matter existed; that the vascular connexion of the internodal spaces was therefore broken up, or was only maintained by a layer of cellular tissue or pith: this doctrine was admitted, and Viscum was supposed to form another illustration of what have been called articulated stems. Some time after, Decaisne published a small work on the woody structure of this plant, in which he contradicted the statement of Dutrochet, and maintained that the vascular or woody portions of the internodal spaces

were continuous, and the state of articulation was solely dependent upon the non-continuity of the vessels of the bark. Dutrochet again averred, before the French Academy, that his views were right. Here, I believe, the matter has rested. I have taken some pains to satisfy myself which of these theories is correct. I have examined portions of the plant, both young and old, and at all portions of the nodal places, and I fully concur with Decaisne in stating that the true woody and vascular structure of Viscum is perfectly continuous through the nodes; that there is no transverse and separating layer of cellular tissue or pith in this portion of the plant, but that the connection of the inner layers of the bark is broken up at the nodes. Viscum album has not an articulated stem, in the proper sense of the word. The vascular structure of Viscum album is by no means so entirely composed of those peculiarly marked and rather elongated cells as is generally drawn and stated. Kieser's representations are often copied, but they only represent a part of the vascular apparatus; no doubt, a great portion of the woody matter is composed of cells quite different from those met with in the wood of Exogens; but if the young wood or first-formed bundles be examined, plenty of very long annular ducts—and (to me) spiral ducts, with the fibre unrollable, however, as far as I have been able to detect—will be found. I may also remark, that the long pleurenchymatous cells surrounding the first-formed vascular bundles are carried along with the latter to the centre of the plant, around the pith of which they may be found, a circumstance somewhat analogous to that stated by Decaisne to take place in Menispermaceæ." (*Annals of Natural History*, ix. 84.)

All the divisions of a stem are in general terms called *branches* (*rami*); but it is occasionally found convenient to designate particular kinds of branches by special names. Thus, the twigs, or youngest shoots, are called *ramuli*, or branchlets, and by the older botanists *flagella;* the assemblage of branches which forms the head of a forest tree is called the *coma: cyma* is sometimes used to express the same thing, but improperly. Shoots which have not completed their growth have received the name of *innovations*, a term usually

confined to mosses. When such a shoot is covered with scales upon its first appearance, as the Asparagus, it is called *turio;* by the old botanists all such shoots were named *asparagi.* When a shoot is long and flexible, it receives the name of *vimen.* This word, however, is seldom used; its adjective being employed instead: thus, we say, *rami viminei,* or *caulis vimineus;* and not *vimen.* From this kind of branch, that called a *virgate* stem, *caulis virgatus,* differs only in being less flexible. A young slender branch of a tree or shrub is sometimes named *virgultum.* When the branches diverge nearly at right angles from the stem, they are said to be *brachiate.* Small stems, which proceed from buds formed at the neck of a plant without the previous production of a leaf, are called *cauliculi.*

Link calls a stem which proceeds straight from the earth to the summit, bearing its branches on its sides, as Pinus, a *caulis excurrens,* and a stem which at a certain distance above the earth breaks out into irregular ramifications, a *caulis deliquescens.*

From the constitution and ramifications of their branches, plants are divided into trees, shrubs, and herbs. If the branches are perennial, and supported upon a trunk, a *tree* (*arbor*) is said to be formed; for a small tree, the term *arbusculus* is sometimes employed. When the branches are perennial, proceeding directly from the surface of the earth without any supporting trunk, we have a shrub (*frutex* or *arbustum,* Lat.), which occasionally, when very small, receives the diminutive name of *fruticulus.* If a shrub is low, and very much branched, it is often called *dumosus* (subst. *dumus*). The *suffrutex,* or *under-shrub,* differs from the shrub, in perishing annually, either wholly or in part; and from the herb, in having branches of a woody texture, which frequently exist more than one year: such is the Mignionette (Reseda odorata) in its native country, or in the state in which it is known in gardens as the Tree Mignionette. The under-shrub is exactly intermediate between the shrub and the herb. All plants producing shoots of annual duration from the surface of the earth are called herbs.

Some botanists distinguish two sorts of stems, the

characters of which are derived from the mode of growth. When a stem is never terminated by a flower-bud, nor has its growth stopped by any other organic cause, as in Veronica arvensis, and all perennial and arborescent plants, it is said to be *indeterminate;* but when a stem has its growth uniformly stopped at a particular period of its existence by the production of a terminal bud, or by some such cause, it is called *determinate.* The capitate and verticillate species of Mint owe their differences to causes of this nature; the stem of the former being determinate, the latter indeterminate.

The point whence two branches diverge is called the *axil,* or, in old botanical language, the *ala:* a term now extended to the angles formed between leaves and the branch on which they grow.

Leaf-buds (*Gemmæ,* Linn.), being the rudiments of young branches, are of great importance in considering the general structure of a plant. They consist of scales imbricated over

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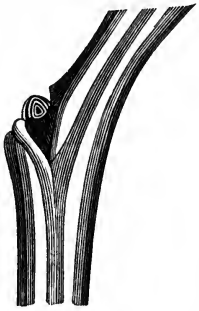

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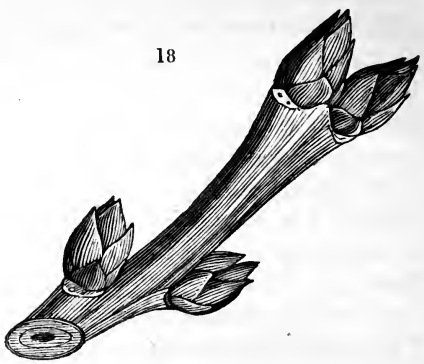


each other, the outermost being the hardest and thickest, and surrounding a minute cellular axis, or *growing point,* which is in direct communication with the woody and cellular tissue of the stem. In other words, they may be said to be growing points covered with rudimentary leaves for the purpose of protection, and to consist of a highly excitable mass of cellular substance, originating in, or connected with, the pith, or cellular portion of the branch, and having a

special power of extension in length. Under ordinary circumstances, the growing point clothes itself with leaves as it advances, and then it becomes a branch; but sometimes it simply hardens as it grows, producing no leaves, but forming a sharp conical projection called a *spine*, as in the Gleditschia, the Sloe, &c. When formed it does not, however, consist of cellular tissue alone; on the contrary, it has the same general internal structure as the perfect branches themselves.

The spine must not be confounded with the prickle or aculeus already described, (p. 164), from which it differs in having a considerable quantity of woody tissue in its structure, and in being as much in communication with the central parts of a stem as branches themselves; while prickles are merely superficial concretions of hardened cellular tissue. Spines occasionally, as in the Whitethorn, bear leaves; in domesticated plants they often entirely disappear, as in the Apple and Pear, the wild varieties of which are spiny, and the cultivated ones spineless. They occasionally branch as in the Gleditschia, thus showing that the power of subdivision is a vital quality inherent in the growing point itself.

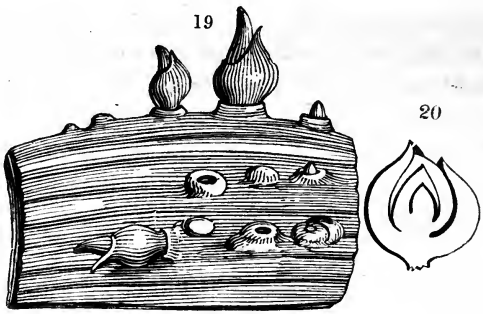
The spadix of the Arum, the receptacle of Nelumbium, all the forms of placenta, and even some styles and stigmata are modifications of the growing point of the bud, and consequently are analogous to unhardened spines.

Linnæus called the bud *Hybernaculum*, because it serves for the winter protection of the young and tender parts; and distinguished it into the *Gemma*, or leaf-bud of the stem, and the *Bulb*, or leaf-bud of the root.

The leaf-bud has been compared by Du Petit Thouars and some other botanists to the embryo, and has even been denominated a *fixed embryo*. This comparison must not, however, be understood to indicate any identity between these two parts in structure, but merely an analogous function, both being formed for the purpose of reproduction; in origin and structure they are entirely different. The leaf-bud consists of both vascular and cellular tissue, the embryo of cellular tissue only: the leaf-bud is produced without fertilisation, to the embryo this is essential: finally, the leaf-bud perpetuates

the individual as well as the species, the embryo continues the species, and not the individual.

The usual, or normal, situation of leaf-buds is in the axil of leaves; and all departure from this position is either irregular or accidental. Botanists give them the name of *regular* when they are placed in their normal station, and they call all others *latent* or *adventitious*. The latter have been found in almost every part of plants; the roots, the internodes, the petiole, the leaf, the flower itself, have all been remarked producing them. On the leaf they usually proceed from the margin, as in Malaxis paludosa, where they form minute granulations, first determined to be buds by Henslow, or as in Bryophyllum calycinum and Tellima grandiflora; but they have been seen by Turpin (*fig.* 19.) proceeding from the surface of the leaf of Ornithogalum. (Fig. 20, represents a vertical section of one of these buds.)



M. Naudin, in the *Annales des Sciences Nat.* vol. xiv. p. 14. describes some small plants of Drosera anglica, which were produced on a leaf on the upper side. They sprang from the cellular tissue, between the midrib and lateral veins near the edge, and were stationed about a line and a half apart. They were from five to six lines in length, and had, it would seem, a stem with alternate leaves, notwithstanding that the Drosera in its natural state is stemless, and only provided with root leaves. Nothing could be observed on the under side of the parent leaf, except a black spot below one of the two stems; there were no roots. The stems issued from the naked cellular tissue, and had no connexion with the vessels of

the leaf. This is undoubtedly an universal rule; buds whether normal, latent, or adventitious, being invariably formed by exciting the peculiar vitality of true cells, and not of tubular forms of tissue; a very important physiological truth.

We are unacquainted with the cause of the formation of leaf-buds; all we know is, that they proceed exclusively from cellular tissue; and if produced on the axis, from the mouths of medullary rays. It would seem as if certain unknown forces were occasionally so exerted upon a vesicle of cellular tissue as to stimulate it into a preternatural degree of activity, the result of which is the production of vessels, and the formation of a centre having the power of lengthening. Any cellular matter, *which is not of a perishable nature*, may be compelled to form buds by a skilful application of heat, moisture, and light. Hence any firm fleshy parts of plants may be employed for propagation, especially fragments of the root, a part which usually possesses an unusually high degree of vitality. A case of the artificial compulsory formation of buds by the scales of a Hyacinth Bulb is mentioned in my *Elements of Botany*, p. 41, fig. 110.

There is, indeed, an opinion, which I believe was that of Mr. Knight, that the sap itself can at any time generate buds without any previously formed rudiment; and that buds depend, not upon a specific alteration of the arrangement of the cellular system, called into action by particular circumstances, but upon a state of the sap favourable to their creation. In proof of this it has been said, that if a bud of the Prunus Pseudo-cerasus, or Chinese Cherry, be inserted upon a cherry stock, it will grow freely, and after a time will emit small roots from just above its union with the stock; at the time when these little roots are formed, let the shoot be cut back to within a short distance of the stock, and the little roots will then, in consequence of the great impulsion of sap into them, become branches emitting leaves.

The leaf-buds of the deciduous trees of cold climates are covered by scales, which are also called *tegmenta*, or sometimes *perulæ;* these afford protection against cold and external accidents, and vary much in texture, thickness, and other characters. Thus, in the Beech, the scales are thin,

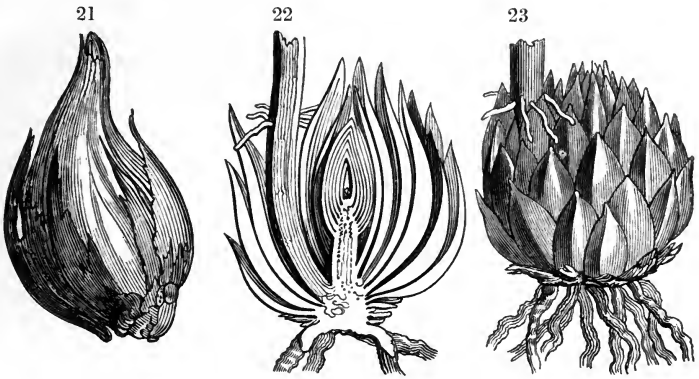
smooth, and dry; in many Willows they are covered with a thick down; in Populus balsamifera they exude a tenacious viscid juice. In herbaceous plants and trees of climates in which vegetation is not exposed to severe cold, the leaf-buds have no dead scales; which is also, but very rarely, the case in some northern shrubs, as Rhamnus Frangula.

The scales of the bud, however dissimilar in their ordinary appearance they may be to leaves, are nevertheless, in reality, leaves in an imperfectly formed state. They are the last leaves of the season, developed at a period when the current of vegetation is stopping, and when the vital powers have become almost torpid. That such is their nature is sufficiently shown by that gradual transition from scales to perfect leaves which occurs in such plants as Viburnum prunifolium, Magnolia acuminata, Liriodendron Tulipifera, and Æsculus Pavia: in the latter the transition is, perhaps, most satisfactorily manifested. In this plant the scales on the outside are short, hard, dry, and brown; those next them are longer, greenish, and delicate; within these others become dilated, are slightly coloured pink, and occasionally bear a few imperfect leaflets at their apex; in succession are developed leaves of the ordinary character, except that their petiole is dilated and membranous like the inner scales of the bud; and, finally, leaves perfect in all their parts complete the series of transitions.

Among the varieties of root is sometimes classed what botanists call a *bulb;* a scaly body, formed at or beneath the surface of the ground, emitting roots from its base, and producing a stem from its centre. Linnæus considered it the leaf-bud of a root; but in this he was partly mistaken, roots being essentially characterised by the absence of buds. He was, however, perfectly correct in identifying it with a leaf-bud, from which it differs in nothing more than in being deciduous, and consisting of scales much more fleshy than in ordinary leaf-buds. In some plants, such as the Tiger Lily, the leaf-buds, in their usual position, in the axils of leaves, acquire a fleshy consistence, and are spontaneously cast off by the stem in the state of true bulbs.

A bulb has the power of propagating itself by developing

in the axils of its scales new bulbs, or what gardeners call *cloves*, (*Nucleus* and *Adnascens* of the older botanists; *Adnatum* of Richard;) which grow at the expense of their parent bulb, and eventually destroy it. In this respect it behaves exactly like a leaf-bud after it has lengthened into a branch. Every true bulb is, therefore, necessarily formed of imbricated scales, and a solid bulb has no existence. The *bulbi solidi*, as they have been called, of the Crocus, the Colchicum, and others are, as we shall hereafter find (see *Cormus*), a kind of subterranean stem: they are distinct from the bulb in consisting not of imbricated scales, but of a solid fleshy mass, itself emitting buds. It has been supposed, indeed, that corms might be buds, the scales of which had become consolidated; but the hypothesis leads to this inadmissible conclusion,—that as the corm or solid bulb of a Crocus is essentially the same, except in size and situation, as the stem of a Palm, the stem of a Palm must be a bulb also; which is absurd. In truth, the bulb is analogous to the bud that is seated upon the corm, and not to the corm itself; a bulb being an enlarged succulent bud without a stem, the corm a subterranean stem with buds on its surface.



Of the bulb, properly so called, there are two kinds.

1. The *tunicated bulb* (*fig.* 21), of which the outer scales are thin and membranous, and cohere in the form of a distinct covering, as in the onion; and, 2. the *naked bulb* (*Bulbus squamosus*) (*fig.* 22. 23.), in which the outer scales are not membranous and united, but distinct and fleshy like the

inner scales, as in *Lilium*. The outer covering of a bulb of the first kind is called the *tunic*.

It has been already stated that there are certain leaf-buds, developed upon stems in the air, and separating spontaneously from the part that bears them, which are altogether of the nature of bulbs. Such are found in Lilium tigrinum, some Alliums, &c. They have been called *bulbilli, propagines, bacilli*, &c. Care must be taken not to follow some botanists, in confounding with them the seeds of certain Amaryllids, which have a fleshy coat; but which, with a vague external resemblance to bulbs, have in every respect the structure of genuine seeds.

Some buds produce leaves only, others flowers only, others both leaves and flowers; the first are the usual state, the second occur in the Peach, Apple, &c., the third in the Lilac and Horsechesnut. These varieties are more different in appearance than in reality, and arise out of the different degrees of growth which the parts within the bud-scales have acquired at the time of expansion of the bud. Moreover, since flowers are as much made up of leaves as branches themselves, as will be hereafter shown, it follows that after all a flower bud is but a leaf-bud in a peculiar condition.

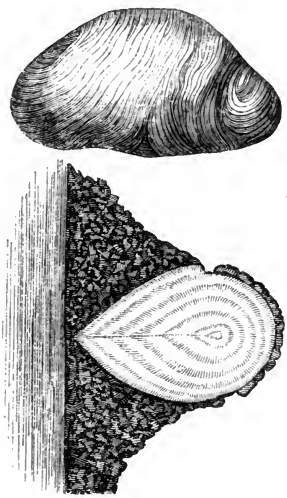
The *tegmenta*, or scales of the bud, have received the following names, according to the part of the leaf of which they appear to be a transformation; such terms are, however, but seldom employed:—

1. *foliacea*, when they are abortive leaves, as in Daphne Mezereum.
2. *petiolacea*, when they are formed by the persistent base of the petiole, as in the Walnut Tree (Juglans regia.)
3. *stipulacea*, when they arise from the union of stipules, which roll together and envelope the young shoot, as in Carpinus, Ostrya, Magnolia, &c.
4. *fulcracea*, when they are formed of petioles and stipules combined, as in Prunus domestica, &c. (*Rich. Nouv. Elem.* 134. ed. 3.)

The manner in which the young leaves are arranged within the leaf-bud is called *foliation*, or *vernation*. The names applied to the various modifications of this will be explained in Glossology; they are of some practical importance for

distinguishing species, genera, and even natural orders; but have, nevertheless, received little general attention. The vernation of the Cherry (Prunus Cerasus) is *conduplicate;* of the Plum (Prunus domestica) *convolute;* of Magnoliads, *convolute;* of Ferns and Cycads, *circinate,* and so on.

Dutrochet called by the name of EMBRYO-BUDS (*fig.* 24.) certain nodules which are commonly found in the bark of the Beech, and some other trees, and which are externally indicated by small tumours of the bark. According to this author such bodies are at first very small and globular, lying in the tissue of the bark, near its surface; he has found some not larger than a pin's head, and thinks they are born in the parenchymatous tissue. "They are at first," he says, "completely free, and isolated in the bark, have a peculiar bark of their own, which is united with that of the parent tree, but which may in the Cedar be easily distinguished by the direction of its fibres.



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"The form of such nodules is variable; sometimes they are rounded, sometimes conical, &c. When in the progress of development, the woody nodules born in the thickness of the bark, bring their wood in contact with that of the tree which bears them, the intermediate bark disappears, being destroyed by the pressure to which it is subjected, and then

the wood of the nodule becomes adherent to the wood of the tree. This adhesion sometimes does not take place for several years. The wood of the nodules is arranged in concentric zones around a common centre, and has both pith and medullary rays; and, however irregular, the form is evidently in all cases a genuine *sphere;* it has all the elements of organisation found in the trunk of the tree, but arranged differently." The side next the wood of the parent tree is thicker than the opposite side, which Dutrochet attributes to its being more immediately in contact with the cambium which nourishes it. In the Cedar of Lebanon the nodules have been seen producing a small branch from the summit. M. Dutrochet regards these nodules as adventitious buds arrested in their formation, and he compares them to the internode of Tamus communis, which forms a tuberous root-like body in that species.

A circumstance to which this physiologist attaches great importance is, that these nodules have an abundance of cambium in the spring, and yet they are not, he says, in communication with the alburnum of the tree; whence he concludes that cambium is elaborated by the bark exclusively. I am not, however, able to reconcile this statement (*Memoires*, i. 311.) with another (p. 304.), that the base of the nodule is "certainement" in adhesion with the wood of the tree.

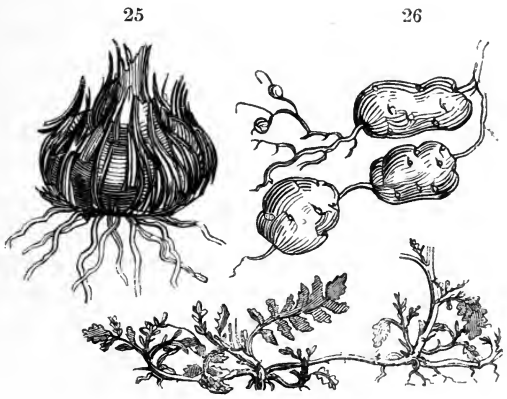
To me it appears that embryo-buds may be best compared to such woody forms of the growing point as occur in spines, the difference being that spines are developed freely in the air, and embryo-buds under pressure within the bark. That they are really of the nature of buds is proved, not only by the Cedar of Lebanon above referred to, but by their being employed, in the case of the Olive Tree, for the purpose of propagation under the name of *Uovoli.* I moreover possess some highly singular forms, brought from Prince of Wales's Island, in which they have acquired a very large size, some of the smaller being as big as the human head, in which all sorts of transitions are observable; some forming spheroidal simple masses, others subdividing, as if about to become branches, and others actually extended into shapeless gouty arms, without, however, producing leaves.

2. Of its External Modifications.

It has already been stated, that the first direction taken by the stem immediately upon its development is upwards into the air. While this ascending tendency is by many plants maintained during the whole period of their existence, by others it is departed from at an early age, and a horizontal course is taken instead; while also direct communication with light and air is essential to most stems, others remain during all their lives buried under ground, and shun rather than seek the light. From these and other causes, the stems of plants assume a number of different states, to which botanists attach particular terms. It seems most convenient to divide the subject into the varieties of—

1. The *subterranean* stem; and
2. The *aerial* stem.

The SUBTERRANEAN stem was confounded by all the older botanists, as it still is by the vulgar, with the root, to which it bears an external resemblance, but from which it is positively distinguished both by its ascending origin, and by its anatomical structure. (*See* Root.)



The following are the varieties which have been distinguished:—

The *Corm, fig.* 25, (*Lecus* of Du Petit Thouars, *Plateau* of De Candolle), is the dilated base of the stem of Monocotyledonous plants, intervening between the roots and the first buds; and forming the reproductive portion of the stem of such plants when they are not caulescent. It is composed of cellular tissue, traversed by bundles of vessels and pleurenchym, and has often the form of a flattened disc. The fleshy "root" of the Arum, that of the Crocus and the Colchicum, are all different forms of the corm. It has been called *bulbotuber* by Ker, and *bulbus solidus* by many others; the last is a contradiction in terms. (*See* Bulb.)

Usually the bud of the corm is at its point: in the Colchicum, however, it is on one side near the base.

The stems of Palms have by some writers been considered as an extended corm, and not a true stem, but this is an extravagant application of the term; or rather an application which reduces the signification of the term to nothing. A corm is a depressed subterranean stem of a particular kind; the trunk of a Palm is, as far as its external character is concerned, as much a stem as that of an Oak. De Candolle applies the name corm only to the stems of Cryptogamous plants, and refers to it the *Anabices* of Necker.

The *Tuber, fig.* 26., is a solid thickened subterranean stem, provided at the sides with latent buds, from which new plants are produced the succeeding year, as in the Potato and Arrow-root. A tuber is, in reality, a part of a subterranean stem, excessively enlarged by the development to an unusual degree of cellular tissue. The usual consequences attendant upon such a state take place; the regular and symmetrical arrangement of the buds is disturbed; the buds themselves are sunk beneath the surface, or half obliterated, and the whole becomes a shapeless mass. Such is not, however, always the case; the enlargement sometimes occurs without being accompanied by much distortion, and the true nature of the tuber stands revealed; this is remarkably the case in the Asparagus Potato. In most, perhaps all tubers, a great quantity of starch is deposited, on which account they are frequently employed as useful articles of food.

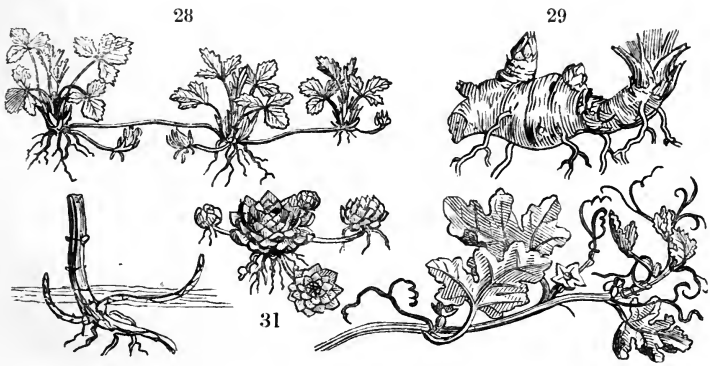
The *Creeping stem, fig.* 27. (*soboles*), is a slender stem, which

creeps along horizontally below the surface of the earth, emitting roots and new plants at intervals, as in Couch grass (Triticum repens.) It differs in nothing whatever from the rhizome, except in being subterranean. This is what in common parlance is called a creeping *root*. It is one of those provisions of nature by which the barren sands that bound the sea are confined within their limits; most of the plants which cover such soils being provided with subterranean stems of this kind. It is also extremely tenacious of life, the buds at every node being very excitable and capable of rapidly renewing the existence of a wounded individual; hence the almost indestructible properties of the Couch grass, and similar plants, by the ordinary operations of husbandry: divisions of its creeping stem, by cutting and tearing, producing no other effect than that of calling new individuals into existence as fast as others are destroyed. A creeping stem is in reality a true Vegetable Hydra, and one of the Sedges, Cyperus Hydra, has obtained its name from the invincible property which it possesses of producing a crop of new heads as soon as one is cut off.

> *Vulneribus fecunda suis* erat illa, nec ullum
> De comitum numero caput est impune recisum,
> Quin gemino cervix herede valentior esset.—Ov.

The term soboles is applied by Link and De Candolle to the sucker of trees and shrubs. (See *Surculus*.)

Of the Aerial stem, the most remarkable forms are the following:—



The *Runner, fig.* 28. (*sarmentum* of Fuchs and Linnæus), is a prostrate filiform stem, forming at its extremity roots and a young plant, which plant itself gives birth to new runners, as in the Strawberry. Rightly considered, it is a prostrate viviparous scape, that is to say, a scape which produces roots and leaves instead of flowers. It has been called *flagellum* by some modern botanists, but that term rather applies to the trailing shoots of the vine.

The *Sucker, fig.* 30, (*surculus*), is a branch which proceeds from the neck of a plant beneath the surface, and becomes erect as soon as it emerges from the earth, immediately producing leaves and branches, and subsequently roots from its base, as in Rosa spinosissima, and many other plants. Link applies the term *soboles* to this form of stem. From this has been distinguished by some botanists the *Stole* (*stolo*), which may be considered the reverse of the sucker, differing in proceeding from the stem above the surface of the earth, into which it afterwards descends and takes root, as in Aster junceus; but there does not appear to be any material distinction between them. Willdenow confines the term *surculus* to the creeping stems of Mosses. By the older botanists a sucker was always understood by the word *stolo,* and *surculus* indicated a vigorous young shoot without branches.

The shoots thrown up from the subterranean part of the stem of Monocotyledonous plants, as the Pineapple for example (the *Adnata, Adnascentia,* or *Appendices* of Fuchsius), are of the nature of suckers.

It may be here remarked, that *stolo* has given rise to the name *stool,* which is applied to the parent plant from which young individuals are propagated by the process of *layering,* as it is technically called by gardeners. The branch laid down was termed *propago* by the older botanists, and the layer was called *malleolus,* which literally signifies a hammer; the name being thus applied, because, when the layer is separated from its parent, its lower end resembles a hammer-head, of which the new plant represents the handle.

The *Offset, fig.* 31, (*propagulum,* Link), is a short lateral branch in some herbaceous plants, terminated by a cluster of leaves, and capable of taking root when separated from the

mother plant, as in Sempervivum. It differs very little from the runner.

The *Rootstock, fig.* 29. (*rhizoma*), is a prostrate thickened rooting stem, which yearly produces young branches or plants. It is chiefly found in Irids and epiphytal Orchids, and is often called *caudex repens.* The old botanists named it *cervix,*— a term now forgotten.

The *Vine, fig.* 32. (*viticula,* Fuchs.), is a stem which trails along the ground without rooting, or entangles itself with other plants, to which it adheres by means of its tendrils, as the Cucumber and the Vine. This term is now rarely employed. De Candolle refers it to the runner or sarmentum; but it is essentially distinct from that form of stem, because it does not root.

The *Pseudobulb* is an enlarged aerial stem, resembling a tuber, from which it scarcely differs, except in its being formed above ground, in having an epidermis that is often extremely hard, and in retaining upon its surface the scars of leaves which it once bore. This is only known in Orchidaceous plants, among which it is very common.

The term *stem* (*caulis*) is generally applied to the ascending caudex of herbaceous plants or shrubs, and not to trees, in which the word *trunk* is employed to indicate their main stem; sometimes, however, this is called *caulis arboreus.* From the *caulis,* Linnæus, following the older botanists, distinguished the *culmus* or *straw,* which is the stem of Grasses; and De Candolle has further adopted the name *Calamus* for all fistular simple stems without articulations, as those of Rushes; but neither of these differ in any material degree from common stems, and the employment of either term is superfluous. This has already been remarked with respect to culmus by Link, who very justly inquires (Linnæa, ii. 235.) "cur Graminibus caulem denegares et culmum diceres?"

If a plant is apparently destitute of an aerial stem, it is technically called *stemless* (*acaulis*), a term which must not however be understood to be exact, because it is, from the nature of things, impossible that any plant can exist without a stem in a greater or less degree of development. All that the term *acaulis* really means, is that the stem is very short.

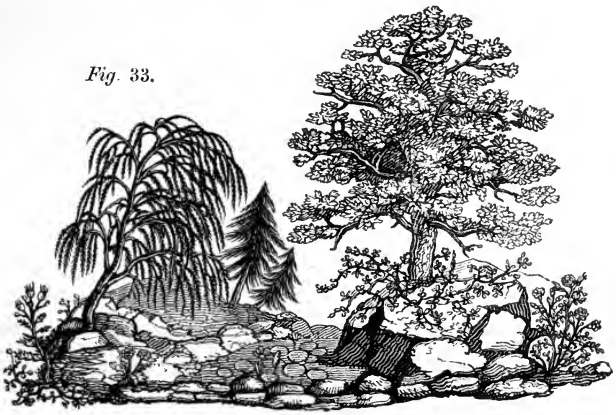
3. Of its Internal Modifications.

In its internal structure the stem of Flowering plants is subject to two principal and to several subordinate modifications. The former are well illustrated by such plants as the Oak and the Cane, specimens of which can be easily obtained for comparison. A transverse slice of the former exhibits a central cellular substance or *pith,* an external cellular integument or *bark,* having often a fibrous lining or *liber,* an intermediate *woody* mass, and certain fine lines radiating from the pith to the bark, through the wood, and called *medullary rays;* this is called EXOGENOUS structure. In the Cane, on the contrary, neither bark, nor pith, nor wood, nor medullary rays, are distinguishable ; but the transverse section exhibits a larger number of holes irregularly arranged, and caused by the section of bothrenchymatous and vascular tissue, and of the mass of woody and cellular substance in which they lie imbedded. This kind of structure is named ENDOGENOUS.

In both cases there is a *cellular* and *vascular system* distinct from each other. The former constitutes the general mass of the stem, the latter is found exclusively in a longitudinal direction, and seems as if plunged amidst the cellular, like roots into earth. The cellular or horizontal system may be compared to the cross threads or *woof* in linen, the vascular or longitudinal system to the *warp.* It is only by a diversity in their respective arrangement that the differences above described are caused. In explaining in detail the peculiar structure of Exogenous and Endogenous stems, I shall continue to consider them with reference to those two systems, because that seems best adapted to the purposes of a teacher. Hereafter some general views upon the subject will be introduced to the reader's notice.

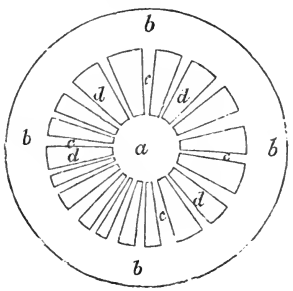
§ 1. *Of the* Exogenous *Structure.*

Fig. 33.



The CELLULAR SYSTEM in an Exogenous stem chiefly occupies the centre and the circumference, which are, however, connected by thin vertical plates of the same nature as themselves. The central part (*a*, *fig.* 34.) is the *pith,* that of the

fig. 34.



circumference (*b*) is the *bark,* and the connecting vertical plates (*c*) are *medullary rays.*

* Pith.

The PITH is a cylindrical or angular column of cellular tissue, arising at the point of separation between the root and stem, and terminating at the leaf-buds, with all of which,

whether they are lateral or terminal, it is in direct or indirect communication. Its tissue, when cut through, almost always exhibits an hexagonal character, and is frequently larger than in any other part. When newly formed, it is green, and filled with fluid; but its colour gradually disappears as it dries up, and it finally becomes colourless. After this it undergoes no further change, unless by the deposition in it, in course of time, of some of the peculiar secretions of the species to which it belongs. It has been contended, indeed, by some physiologists, that it is gradually pressed upon by the surrounding part of the vascular system, until it is either much reduced in diameter or wholly disappears; and in proof of this assertion, the Elder has been referred to, in which the pith is very large in the young shoots, and very small in the old trunks. Those, however, who entertain this opinion, seem not to consider that the diameter of the pith of all trees is different in different shoots, according to the age of those shoots;—that in the first that arises after germination, the pith is a mere thread, or at least of very small dimensions—that in the shoots of the succeeding year it becomes larger—and that its dimensions increase in proportion to the general rapidity of development of the vegetable system: the pith, therefore, in the first-formed shoots, in which it is so small compared with that in the branches of subsequent years, may not be small because of the pressure of surrounding parts; it may never have been any larger. It is, however, probable that by degrees the calibre of the pith is lessened by the contraction of the fibrous column of wood that incloses it. This would seem to be so from the following statement by the Rev. P. Keith:—

"On the 1st of June, 1836, I separated from the stool of an ash-stock a stem of three years' growth. It measured about nine feet in height, the growth of each year being distinctly marked, and measuring each about three feet in length. The upper shoot, that is, the shoot of 1835, had a diameter of $\frac{3}{8}$ths of an inch, with a pith of $\frac{1}{4}$th at the widest. The middle shoot, that is, the shoot of 1834, had a diameter of $\frac{7}{12}$ths of an inch, with a pith of $\frac{1}{6}$th; and the lower shoot, that is, the shoot of 1833, had a diameter of $\frac{2}{3}$ths of an inch,

with a pith of $\frac{1}{10}$th. Now, as the shoots of the several years were equally luxuriant, and the youngest a year old, the pith ought, by hypothesis, to have been of the same dimensions in all of them. Yet it was gradually smaller and smaller from the youngest to the oldest, though it was undoubtedly of equal diameter in the first year's growth of each. For the shoot of a single year, from a different stock, gave a diameter of pith equal to that of the upper shoot of the above stem; and poles of twelve years old gave still a diminishing diameter when inspected towards the base." Whence he inferred that the pith keeps shrinking, from one cause or other, long after the period of the first year's growth. This may be admitted without acquiescing in the statement formerly made by Mirbel, that pith diminishes in diameter, "by being converted first into longitudinal tubes and then into wood," an hypothesis which seems to rest on no satisfactory observation.

According to Dutrochet and others, the pith does not extend into the root of Exogens; and it certainly occurs there, when woody, in very minute quantity, if at all. Mr. Keith, however, seems to have shown that its presence has been sometimes overlooked, for he finds it in many seedlings. Of this he gives the following examples:—

"I took up a seedling of the Beech Tree, Fagus sylvatica. The seed leaves were still attached to it, and were fully expanded; and the stem on the horizontal section was divisible into bark and bundles of woody fibre, together with a central pith and spirals. All this is what was to be expected; and the next thing remaining to be done was the inspection of the roots of the said seedlings, which was now undertaken. In the above specimens, this root measured from two to three inches in length, with a good many lateral fibres, and on a horizontal section exhibited like the stem, a bark, a circular layer of woody fibre, but without spirals, and a central or axial mass, which mass differed in nothing visible from the central mass of the stem, whether as relative to its colour or to its spongy and cellular texture. On this account I have no hesitation in pronouncing it to be a true and legitimate pith, though lodged in the descending axis. If it be

said, that owing to the elevation of the seed leaves in the above cases, the place of the collum must have been rendered doubtful, and that of the commencement of the real root uncertain, then I will present a case from which doubt is altogether excluded.

"On the 15th of July, 1836, I stumbled on a seedling of Corylus Avellana. I took it up with much care and found that the seed lobes and half of the investing shell were still attached to it. The stem measured seven inches in length, with three or four leaves. The root measured three or four inches in length, with many lateral fibres; and the diameter of the plant, at the widest, was about one-eighth of an inch. In taking a longitudinal section of a portion of the root and stem so as to pass through the collum, which could not be mistaken, as the lobes never rise above the level of the soil, it was evident that the pith, strictly cellular and under the aspect of a fine thread, descended into the root, without any node or interruption, or breach of continuity whatever, and without any appreciable difference beyond that of colour. Above the collum it was of a deep red; below it was of a pale green. If any doubt remains in the mind of the reader as to the accuracy of this statement, I shall be very glad if he will have the goodness to repeat the experiment on a seedling of the same species and of the same age, and to say what he thinks of it then. With regard to myself, I hold it to be a most satisfactory proof of the existence of a pith in the descending axis even of Exogens. It may be seen equally well in the root of seedlings of the Oak and Ash, but without the peculiarity of the red and green colours."

The pith is always, when first forming, a uniform compact mass, connected without interruption in any part; but the vascular system sometimes developing more rapidly than itself, it occasionally happens that it is either torn or divided into irregular cavities, as in the Horse Chestnut, the Rice-paper plant, and many others; or that it is so much lacerated as to lose all resemblance to its original state, and to remain in the shape of ragged fragments adhering to the inside of the vascular system: this is what happens in Umbelliferous and other fistular-stemmed plants.

In certain Trees, of which the Walnut is an example, the pith is regularly broken up into small horizontal chambers separated by thin discs. It is not, however, so when young, but the structure belongs to its advanced age. Professor Morren has investigated the history of this curious structure in the *Annals of Natural History*, vol. iv. The following are extracts from his interesting paper, which deserves to be studied *in extenso*. He thus describes the changes observed in the pith of the Silver-spotted Begonia (B. argyrostigma.)——"*First period.*—The pith is continuous, full, compact, without interruption of continuity. It is composed of cells which have been spherical, and which are become prismatic by their mutual compression. These cells lengthen by degrees transversely, and end by being disposed thus in horizontal planes. At this period the cell is filled with a liquid, and fecule; it overflows with nutritive substance; its pith appears green, like the germinating cotyledon of a plant.——*Second period.*—The pith is become more extended by the development of the branch; the fecule changes into alimentary juice; it dissolves by the operation of nutrition (does it become gum?), first disappearing from the central cells of the pith, where the nuclei are formed at the same time with some granules of chlorophylle. By the loss of this nutritive substance, such inorganic substances as salts obey the forces of the inorganic world, and crystallise by degrees; the crystals being formed in the cells. The intercellular liquid, or the elaborated fluid which originates in the descending sap, and which has been transmitted to the pith by the medullary rays, is absorbed to the grain of the bud. The diminution which results from absorption begins to dry up the cells, which separate from one another horizontally. Then the slit is formed. We might say that the force of suction, wrought by the bud, took place in the axis of the stalk; it is, in fact, in this axis that the slit is first formed. These slits are at first at great distances from one another.——*Third period.*—The same facts continuing, results accumulate on results. The circumference alone of the pith still contains any fecule, but this nutritive substance has completely disappeared from the remainder of the pith. The water of vegetation, the

elaborated fluid of the sap, is more and more subtracted towards the bud, the pith dries more and more, the slits are multiplied and grow so large as to be true lenticular cavities, which leave between them medullary discs. The latter then are formed by layers of cells nicely separated one from another, out of a mass primitively common, but without laceration of the partitions; these, at first double for the contiguous cells, are now become isolated. At the same time the pith loses its green colour and becomes of a clear yellow, by the drying up of the membranes of the cells, and brilliant points are formed; these are numerous crystals which originate from the diminution of the liquid in which their elements were originally dissolved. It is so true that these changes take place in this manner, that if we cut a stalk of Begonia argyrostigma longitudinally, when it is fresh and the pith only slit, at the end of two days we see the slits become lenticular cavities, and the medullary discs are formed at the same time that the pith drying up passes from green to yellow, and the crystals make their appearance. In fact the sap is lost by evaporation, as in the plant it disappears by the suction of the bud; but it is lost, and the same causes bring about the same results.——*Fourth period.*—The bud being developed and the branch formed, the pith is become useless. It is deprived of all its juice; its cellular tissue, whose cells are become large, is dried up completely; the desiccation has separated all the layers of cells, and a considerable number of discs have been formed; brown dry discs formed by the empty cells, without and within which the salts have crystallised in different forms. This is the period of death."

The Walnut Tree offered another instance of discoid pith, the gradual formation of which Professor Morren also traced, and thus describes:—"The compact pithin the Walnut Tree is composed of a number of small cells nearly in the form of cubes, all equal to one another, white, transparent, having very few globules, but containing at a very early period masses of small crystals, or true muriform calculi, which occupy the centre of the cells. At a later period, when the pith separates into discs, and dies, the cells undergo very

few modifications.—I sought on a Walnut Tree a branch whose young shoot was very long. The terminal bud was separated from the last leaf but one by an internode of nine centimetres in length. Then came a leaf at five centimetres distance, and another eleven centimetres lower down. On this branch the pith was full at twelve centimetres lower than the terminal bud; but at each leaf, bearing a bud in its axil, the pith was perforated by some lenticular cavities. Here the action of the bud is evident, and better proof could not be brought that it is to the absorbing action of the bud that we owe the division of the pith into discs.—I cut this long branch into two and dried it. The next day the compact pith had lost its liquid to so great a degree that the stem was hollowed into a gutter; the slits were greatly increased, but the membrane formed by the pith was also seen dried up and covering the bottom of the gutter formed by the half of the stem slit longitudinally; this membrane was also raised by as many hollow vesicles as there would have been lenticular cavities if the stalk had remained entire; here is a manifest proof that there is in the constitution of the pith a predisposition to separate thus into discs, and this predisposition consists in nothing more than the manner in which the layers of the cells are placed." (See additional observations and anatomical figures in the work above referred to.)

Sometimes the pith is more compact at the nodes than in the internodes, as in the Ash; whence an idea has arisen that it is actually interrupted at those places: this is, however, a mistake; for in general there is no interruption of continuity, but a mere alteration in compactness. It does however sometimes happen, that the pith takes a large development at the nodes, so as to interrupt the vascular system of the internodes. This occurs in what are called articulated stems, as in Piper, &c., and in the Vine when young. Dutrochet regards such cases as evidence that each internode is an independent creation in the beginning, and that it is only after having been growing for a period of time, varying in different cases, that the internodes become connected by woody formations. The Miseltoe, however, on which he relies for

supporting this hypothesis, does not justify the conclusion, as has been already shown.

It seldom happens that any part of the vascular system intermixes with the pith, which is usually composed of cellular tissue exclusively; but in Ferula and the Marvel of Peru, it has been proved by Mirbel and De Candolle, that bundles of woody fibre are intermixed; in Nepenthes there is a considerable quantity of spiral vessels scattered among the cellular tissue of the same part; and many other cases of a similar kind are now known. In Nyctagos generally, in Pepperworts (Piperaceæ), Cycads, Chloranths, &c., this occurs, and has been made by Professor Schultz the character of a division in his Natural System of Botany, called by him *Synorgana dichorganoidea;* but such cases may be found in Loranthus, and are not uniform in the orders quoted: in Boerhaavia repanda, for example, the pith contains no bundles of vascular tissue, but is *filled with fistulæ containing very soft, lax, spheroidal, cellular tissue, surrounded by smaller, harder, and more cubical tissue, which passes into the medullary rays;* a most curious organisation.

* * Bark.

The BARK is the coating of the stem immediately above the wood, to which it forms a sort of sheath, and from which it is separable without difficulty at certain seasons. But, although it appears as an independent formation, it is, in reality, organically connected with the wood by the processes of cellular tissue, which, under the name of medullary rays, pass through the wood, and lose themselves in the thickness of the bark. Bark is usually distinguished into *cortical* or *cellular integument,* under which name is comprehended the whole of the external parenchymatous part, and *liber* or *inner bark,* a name used to denominate the fibrous woody portion lying next the alburnum, and this is extremely convenient for all common purposes. The cortical integument thus defined belongs to the horizontal system, and the liber to the longitudinal, the two standing in the same relation to each other as wood to pith—the cortical integument

being an outer pith, the pith an interior bark, the liber being the wood of the bark, and the wood the liber of the pith.

In an anatomical point of view, the observations of Mohl are the best and most complete which have hitherto been made upon this very important subject: they, and many more of considerable value, by Dutrochet, Link, and others, have given rise to a peculiar nomenclature for the parts of the bark, in order to avoid the somewhat indefinite ideas which attach to the older terms.

Bark may be described anatomically as composed of four separate parts:—1. The *Epidermis*, which is continuous with that of the leaves, resembling what is found upon their veins, like it composed of cells a little lengthened, and rarely furnished with stomates; it often bears hairs. 2. The *Epiphlœum* of Link, *Phlœum* or *Peridermis* of Mohl, consisting of several layers of thin-sided tabular cells, rarely coloured green. In this part Achille Richard distinguishes an inner colourless layer which he calls the *Mesoderm*. 3. The *Mesophlœum* of Link, or *herbaceous* or *cellular integument* of others, composed of cells usually green, and placed in a different direction from those of the epiphlœum; sometimes, as in the Cork tree (Quercus Suber), containing cellular concretions. 4. The *Endophlœum* or *Liber*, of which a part is cellular and a part composed of woody tubes. The cellular face of the liber, which serves to connect it with the medullary plates, A. Richard distinguishes by the name of *Subliberian layer*, or *Endoderm*. These are modified differently in different trees; and the appearances of Cork in many plants, of thin white lamellæ or hard plates in others, are so produced. Usually each stratum has a separate growth, which takes place by the addition of new matter to its interior; thus the endophlœum, or liber, grows next the alburnum, the mesophlœum next the endophlœum, and the epiphlœum next the mesophlœum; the epidermis does not grow at all. Such growth is often indicated by concentric circles, which correspond in each layer with the zones of wood.

When the substance called *Cork* is formed, the epiphlœum consists of polyhedral cells, which multiply with unusual

rapidity and in great quantities. It does not appear to have any communication by lateral passages with the interior of the plant; although Dutrochet represents them to exist in Ulmus suberosa, where I cannot find them. After a certain age, it exfoliates, in the Cork Tree, but in such plants as the Maple (Acer campestre), the Elm, &c., it is simply rent and thrown off piecemeal. In the Birch, the Cherry, and similar trees, it forms annually only a few layers of tabular cellular tissue, *arranged in transverse rows,* which separate at a certain age into thin silvery lamellæ: these have been improperly confounded with the epidermis. The cause of the separation of the lamellæ of the epiphlœum of the Birch is found in the development, between the lamellæ, of a layer of thin-sided cells, less compactly arranged, and easily separating into a fine powder when disturbed.

As strata of cellular tissue, in a peculiar state, may form between the lamellæ of the Birch and other such trees, so may it in other parts of the bark. This causes the sloughing of hard thin plates from the bark of the Plane tree; which Mohl explains thus:—Up to its eighth or tenth year, the bark of the Plane tree is like that of the Beech; at that period there forms in different parts of the liber a stratum of tabular cells, in all respects analogous to those of the epiphlœum. This new epiphlœum is not exactly parallel with that of older date, which exists at the surface of the bark, and cuts off an exterior portion, which then dies and drops off in the manner with which we are all familiar. The scales produced by this formation of epiphlœum inside the liber or mesophlœum Mohl calls *Rhytidoma,* from ῥυτις, a wrinkle. (*Ann. des Sciences,* N. S. ix. 290.)

In some plants the epiphlœum forms regular strata, parallel with the axis of the stem, and afterwards separates into strips analogous to those of the liber, as in the Juniper, Callistemon lophanthus, &c. In others, a portion of the liber is really thrown off annually, as in the Vine, the Honeysuckle, &c.

Hence in exogenous trees, the thickness of the bark is annually diminished by one of two causes; either by an exfoliation of the external and dead portions of the epiphlœum only, or by a formation of a second epiphlœum, or false cork,

among the liber, the result of which is the throwing off the parts of the bark lying over it as soon as they die.

So long as the parts of the bark remain alive, they give way to the expansion of the wood within it, by adding new tissue to themselves, as has been already stated: but when they die, they are necessarily torn into clefts, rents, or ribands, as we find in the trunks of trees.

These statements, taken from the writers above referred to, although valuable as far as they go, by no means lead to satisfactory general conclusions, and demand much more investigation. The bark has never, in fact, received the attention which its great importance demands.

When stems are old, the bark usually bears but a small proportion in thickness to the wood; yet in some plants its dimensions are of a magnitude that is very remarkable. For instance, specimens of Abies Douglasii have been brought to Europe twelve inches thick, and these are said not to be of the largest size.

Air cells and Vasa propria are exceedingly common in the bark, but there is no authenticated instance of any spiral or other vessels having been found in it; except in Nepenthes, in which they occur in almost every part, and exist in no inconsiderable numbers in the bark.

* * * Liber.

It will have been seen that the only part of the bark in which woody or longitudinal tissue occurs is the liber or endophlœum. Here it is often very abundant, and exceedingly tough and thick-sided; in consequence of which it is of great value for many useful purposes. When freed from the cellular tissue adhering to it, it is often manufactured into cordage, especially in trees and shrubs of the natural order Malvaceæ. The Russia mats of commerce are manufactured from the thin laminæ into which the endophlœum of the Lime Tree (Tilia europæa) readily separates. The Lace bark of Jamaica, remarkable for its beautiful lace-like appearance when gently pulled laterally, and for its great toughness, whence it is twisted into whip-lashes, is the laminated liber of Lagetta lintearia.

The liber does not always, or perhaps often, form a compact layer of tubes; on the contrary, its tissue has a wavy direction, and lies in bundles which touch each other here and there, and can be readily separated. This is in reality the same structure as occurs in the zones of wood, only that it is much more conspicuous, and it arises from the same cause, namely, the necessity for the woody tissue of the liber leaving innumerable passages between its tubes for the free passage of the cells belonging to the horizontal system, and passing from the cortical integument into the medullary rays.

The tissue of the liber consists of nothing but pleurenchym, of great toughness owing to its very thick sides, and of laticiferous vessels. No vascular tissue, properly so called, has been observed in it, with the solitary exception of Nepenthes. The toughness of the liber-tubes is probably given them in order that they may possess the strength, combined with flexibility, which their position near the circumference of a branch renders necessary.

Anomalous structure in liber has been little observed; the most singular instance of it is that mentioned by Decaisne (*Comptes rendus*, v. 393.) who says that in Menispermads the liber is only formed for the first year, and is *afterwards covered over by new wood;* and consequently is found near the centre round the pith, and not at the circumference.

* * * * Cambium.

Beneath the liber, and above the wood, is interposed in the spring a mucous viscid layer, which, when highly magnified, is found to contain numerous minute transparent granules, and to exhibit faint traces of a delicate cellular organisation. This secretion is named the CAMBIUM, and appears to be exuded both by the bark and wood; Dutrochet says only by the former, founding his opinion upon the presence of cambium in bark nodules, which, he says, have no communication with the wood of the parent tree; see page 177.

Although the name of Cambium was originally given to the mucous secretion found in the spring between the bark and wood of Exogens, yet it is in truth nothing more than the organisable matter, or "generative sap," which occurs

in all the living parts of plants, and out of which new organs are formed. (See p. 7). It is, therefore, here introduced in connection with bark, merely in compliance with old custom. Its history has been elaborately investigated by De Mirbel, to whose papers in the *Comptes rendus, Annales des Sciences,* and *Archives du Museum,* the reader is referred. There is also a short abstract of one of his papers in the *Annals of Natural History,* vol. vi. p. 330.

**** Medullary Rays.

The cellular system of the pith and bark are, in the embryo and youngest shoots, in contact; but the woody system, as it forms, gradually interposes between them, till after a few weeks they are distinctly separated, and in very aged trunks are sometimes divided by a space of several feet; that is to say, by half the diameter of the wood. But whatever may be the distance between them, a horizontal communication of the most perfect kind continues to be maintained. When the woody system is first developed in the cellular system, separating the pith from the cortical integument, it does not completely separate them, but pushes aside a quantity of cellular tissue, pressing it tightly into thin vertical radiating plates: as the woody system extends, these plates grow outwardly, continuing to maintain the connection between the centre and the circumference. Botanists call them *medullary rays* (or *plates*); and carpenters, the *silver grain.* They are composed of muriform cellular tissue (Plate I. fig. 7.), often not consisting of more than a single layer of cells; but sometimes as in Birthworts, (Aristolochia), the number of layers is very considerable. In horizontal sections of an Exogenous stem, they are seen as fine lines radiating from the centre to the circumference; in longitudinal sections they produce that glancing satiny lustre which is in all discoverable, and which gives to some, such as the Plane and the Sycamore, a character of remarkable beauty.

No vascular tissue is ever found in the medullary rays, unless those curious plates described by Griffith in the wood of Phytocrene gigantea, in which vessels exist, should prove to belong to the medullary system.

The VASCULAR SYSTEM in an Exogenous stem is confined to the space between the pith and the bark, where it chiefly consists of ducts, and pitted or woody tissue collected into compact wedge-shaped vertical plates, *fig.* 34. the edges of which rest on the pith and bark, and the sides of which are in contact with the medullary rays. It consists of *liber*, *wood*, and the *medullary sheath*.

* Medullary Sheath.

That portion of the vascular system which is first generated is in immediate contact with the pith, to which it forms a complete sheath, interrupted only by the passage of the medullary rays through it. It consists of spiral vessels and woody tissue intermixed, and forms an exceedingly thin layer, called the *medullary sheath*. This is the only part of the vascular system of the stem in which spiral vessels are ordinarily found; the whole of the vessels subsequently deposited over the medullary sheath being bothrenchymatous tissue, with a few exceptions. The medullary sheath establishes a connection between the axis and all its appendages, the veins of leaves, flowers, and fruits, being in all common cases prolongations of it. It has been remarked by Senebier, and since by De Candolle, that it preserves a green colour even in old trunks, which proves that it still continues to retain its vitality when that of the surrounding parts has ceased.

** Wood.

The vascular system of a stem one year old consists of a zone of wood lying between the pith and the bark, lined in the inside by the medullary sheath, and separated into wedge-shaped vertical plates by the medullary rays that pass through it. All that part of the first zone which is on the outside of the medullary sheath is composed of woody tissue and vessels intermixed in no apparent order; but the vessels are generally either in greater abundance next the medullary sheath, or confined to that side of the zone, and the woody tissue alone forms a compact mass on the outside. The second year another zone is formed on the outside of the

first, with which it agrees exactly in structure, except that there is no medullary sheath; the third year a third zone is formed on the outside of the second, in all respects like it; and so on, one zone being deposited every year in cold countries as long as the plant continues to live. As each new zone is formed over that of the previous year, the latter undergoes no alteration of structure when once formed. Wood is not subject to a distension by a force beneath it, as the bark is; but, whatever the first arrangement or direction of its tissue may be, such they remain to the end of its life. The formation of the wood is, therefore, the reverse of that of the bark; the latter increasing by addition to the inside of its strata, the former by successive deposits upon its outside. It is for this reason that stems of this kind are called Exogenous (from two Greek words, signifying to grow outwardly). According to Dutrochet, each zone of wood is in these plants separated from its neighbour by a layer of cellular tissue, forming part of the system of the pith and bark: but although this is true in certain plants, such as arborescent nettles and others, it is by no means a general law.

After wood has arrived at the age of a few years, or sometimes even sooner, it acquires a colour different from that which it possessed when first deposited, becoming what is called *heartwood* or *duramen*. For instance, in the beech it becomes light brown, in the oak deep brown, in Brazil wood and Guaiacum green, and in ebony black. In all these it was originally colourless, and owes its different tints to matter deposited gradually in all parts of the tissue; as may be easily proved by throwing a piece of heart-wood into nitric acid, or some other solvent, when the colouring matter is discharged, and the tissue recovers its original colourless character. That part of the wood in which no colouring matter is yet deposited, and consequently that which, being last formed, is interposed between the bark and duramen, is called *alburnum*. The distinction between these is physiologically important, as will hereafter be explained.

Age of Exogens.

Each zone of the vascular system of an Exogenous stem being the result of a single year's growth, it should follow that, to count the zones apparent in a transverse section is sufficient to determine the age of the individual under examination; and further, that, as there is not much difference in the average depth of the zones in very old trees, a certain rate of growth being ascertained to be peculiar to particular species, the examination of a mere fragment of a tree, the diameter of which is known, should suffice to enable the botanist to judge with considerable accuracy of the age of the individual to which it belonged. It is true, indeed, that the zones become less and less deep as a tree advances in age; that in cold seasons, or after transplantation, or in consequence of any causes that may have impeded its growth, the formation of wood is so imperfect as scarcely to form a perceptible zone: yet De Candolle has endeavoured to show in an able paper, *Sur la Longévité des Arbres,* that the general accuracy of calculations is not much affected by such accidents; occasional interruptions to growth being scarcely appreciable in the average of many years. This is possibly true in European trees, and in those of other cold or temperate regions in which the seasons are distinctly marked; in such the zones are not only separated with tolerable precision, but do not vary much in annual dimensions. But it is not absolutely true in Europe, as is proved by the Beet, whose root forms several zones during the growth of one year; and in many hot countries the difference between the growing season and that of rest, if any occur, is so small, that the zones are as it were confounded, and the observer finds himself incapable of distinguishing with exactness the formation of one year from that of another. In the wood of Guaiacum, Phlomis fruticosa, Metrosideros polymorpha, and many other Myrtleblooms (Myrtaceæ), for instance, the zones are extremely indistinct; in some Bauhinias they are formed with great irregularity; and in Stauntonia latifolia, some kinds of Ficus, certain species of Aristolochia, as A. labiosa, and many other plants,

they are so confounded, that there is not the slightest trace of annual separation. It is also to be remarked, that in Zamias we seldom find more than two or three zones of wood, whatever may be the age of the individual; and yet it appears from Ecklon's observations, that a Zamia, with a trunk only four or five feet high, can scarcely be less than two or three hundred years old. (*Lehm. Pugill.* vi.) According to Decaisne (*Comptes rendus,* v. 393.) the zones of wood in Menispermads each result from the growth of several years. Moreover it is certain that in tropical countries some trees will form from one to four well defined zones of wood during the growth of a single twelvemonth.

With regard to judging of the age of a tree by the inspection of a fragment, the diameter of the stem being known, a little reflection will show that this is to be done with great caution, and that it is liable to excessive error. If, indeed, the zones upon both sides of a tree were always of the same, or nearly the same thickness, much error would, perhaps, not attend such an investigation; but it happens that, from various causes, there is often a great difference between the growth of the two sides, and consequently, that a fragment taken from either side must necessarily lead to the falsest inferences. For example, I have now before me four specimens of wood, taken almost at hazard from among a fine collection, for which I am indebted to the munificence of the East India Company. The measurements of either side, and their age, as indicated by the number of zones they comprehend, are as follows:—

	Diameter of			Real Age, or No. of Zones.
	Side A.	Side B.	Total.	
Benthamia fragifera .	9 lines	36 lines	45 lines	40
Pyrus foliolosa . .	8 lines	22 lines	30 lines	36
Magnolia insignis . .	11 lines	20 lines	31 lines	17
Alnus napalensis . .	11 lines	23 lines	34 lines	8

Now, in the first of these cases, suppose that a portion of the side A. were examined, the observer would find that each zone is 0·225 of a line deep; and, as the whole diameter of the stem is 45 lines, he would estimate the side he examined

to be 22·5 lines deep; consequently, he would arrive, by calculation, at the conclusion, that, as his plant was one year growing 0·225 of a line, it would be a hundred years in growing 22·5 lines, while, in fact, it has been only forty years. And so of the rest.

When we hear of the Baobab trees of Senegal being 5150 years old, as computed by Adanson, and the Taxodium distichum still more aged, according to the ingenious calculations of Alphonse De Candolle, it is impossible to avoid suspecting that some such error as that just explained has led to such excessive calculations.

There is, however, no doubt that Exogenous trees acquire an age which may seem incredible to those who do not recollect how much their peculiar way of life favours an incessant and indefinite renewal of vegetative force for periods of unknown duration. We have, in fact, good historical proof of at least the following cases :—

An Ivy, near Montpellier . . .	433 years
Lime Trees, near Friburg . . .	1230 „
Neustadt . .	800 „
Larch	576 „
Cedars on Mount Lebanon .	6—800 „
Oaks, at least.	1000 „

In the garden of the late Sir Robert Vaughan, at Nannau, in Merionethshire, there once existed a gigantic Oak, which was said by tradition to have been the very tree in which Owen Glendwr confined the Welch Chieftain, Howel Sale, taken prisoner by him in the time of Henry IV. Let us suppose this tree, which was of course hollow, to have been only three feet in diameter in 1410 (and it could not have been less, and was probably much more), and let us take the annual growth of old Oak trees to be one inch of semi-diameter in twenty years; it must in that case have been 360 years old in 1410—to this add 403, the number of years that intervened between 1410 and 1813, when it was blown down, and we shall obtain a total age of 763 years. It was, no doubt, much older.*

* There is an apocryphal story of an oak tree having been felled in the Ardennes, within whose trunk were found coins struck 276 years before the foundation of Rome. That tree was, therefore, estimated to have been 3600 years old.

But the mere size of Exogenous trees testifies to their occasional high antiquity.

The Chesnut (Castanea vesca) of Mount Ætna, called the Castagna di cento cavalli, because 100 horsemen can find shelter in its hollow, is 180 feet in circumference.

There is at this day in the village of Bujukdere, near Constantinople, a hollow Plane tree (Platanus orientalis), 150 feet in circumference, and 80 feet in circumference inside.

The Courbaril tree (Hymenæa Courbaril), sometimes acquires, in the West Indies, a diameter of 20 feet.

The Ceiba tree (Bombax pentandrum) also called the Buttress tree, is sometimes so large that fifteen men can hardly embrace it with extended arms.

Martius figures (see *Vegetable Kingdom*, p. 551.) enormous Brazilian Hymenæas, 84 feet in circumference at the butt, and, as he thinks, referable to the age of Homer!

Douglas saw Pinus Douglasiana 193 feet high, on the coast of Oregon, near Cape Orford, and Pinus Lambertiana 226 feet high.

This is sufficient to establish the power, on the part of Exogens, of attaining a very high antiquity, without admitting the miscalculations of De Candolle, as regards the Senegal Baobabs, upon which Professor Henslow has very properly commented thus:—

"Before we quite dismiss these wonders, we must mention that M. De Candolle appears to have somewhat exaggerated, or, as some may think, improved upon, the account of the Baobab given by Adanson in his *Familles des Plantes*. That excellent observer stated the inscriptions which he examined to have been on the *surface* of the tree, but M. De Candolle has somehow made out that he had detected them in the *inside!*

"'The Baobab,' says he, 'is the most celebrated instance of extreme longevity which has hitherto been noticed with any degree of accuracy. In its native country it bears a name which signifies "a thousand years;" and, contrary to what is usual, this name expresses what is in reality short of the truth. Adanson has noticed one in the *Cape de Verd*

Islands which had been observed by *two English travellers* three centuries earlier: he found *within* its trunk the inscription which *they* had engraved there covered over by *three hundred woody layers*, and thus was enabled to estimate the bulk by which this enormous plant had increased in three centuries.' ! !—p. 1003.

"Let us compare this account with Adanson's own words, observing the passages we have noted in italics.

" 'Those which I saw in 1749 on the *Isles de la Madeleine*, near Cape Verd, with inscriptions of *Dutch* names, such as Rew, and other, *French* names, the former dating from the fourteenth and the latter from the fifteenth century, which inscriptions I renewed, merely adding below them, "renewed in 1749," were then about six feet in diameter. These same trees were seen in 1555, that is to say, two hundred years earlier, by Thevet, who notices them in the account of his *Voiage aux Teres Antarktikes*, describing them merely as "fine trees," without mentioning their thickness, which must at least have been three or four feet, judging from the little space occupied by the characters forming the inscription; they had, therefore, enlarged about two or three feet in *two hundred* years.'—*Familles des Plantes*, Preface, p. ccxvi."

Of all natural orders of Plants that of Conifers exhibits the most certain and instructive instances of longevity, concern- which Professor Zuccarini's observations deserve to be quoted.

"The Common Spruce and Silver Firs, and the Scotch Pine not unfrequently live above 200 years; and the Alpine Pines, the Larches, and Cypresses are frequently at least 500 years old. De Candolle (*Physiolog. Vegetal.* ii. p. 1001.) estimates the age of the largest yews as much greater. Assuming that in the transverse section of this tree, including both semi-diameters, each annual ring of the first 150 years of growth has a thickness of a French line, and afterwards something less, he demonstrates from the given measurements of the largest yews, especially in Great Britain, that the stem of one growing at Fountains Abbey, in Yorkshire, which was measured by Pennant, in 1770, and found at that time to have a circumference of 26·6 feet,

would contain 1214 annual rings, and would consequently be that number of years old. Another in the churchyard of Crowhurst, in Kent, would possess 1458 annual rings; one in the churchyard of Fotheringhay, in Scotland, measuring 58·6 feet in circumference, 2588; and one in the churchyard of Brayburn, in Kent, according to the measurement of Evelyn, in 1660, would at that time have attained an age of 2880 rings or years.

"Lastly, enormous trunks of Taxodium distichum are met with both in Florida and in Southern Louisiana, as well as in Mexico. Michaux mentions some of these stems of forty feet in circumference above the rounded, enlarged base, which was three or four times that size. The so-called Cypress of Montezuma, in the garden of Chapultepec (Mexico), measures forty-one feet (English) in circumference. But all these dwindle to nothing before the gigantic trunk near Santa Maria de Tesla, in the province of Oaxaca, which was first mentioned by Exter, who found its circumference to be 117·10 feet (French). With respect to this account, however, De Candolle thought that either several trees might have grown together, or were this not the case, that the measurement had been taken round the dilated base of the trunk. By the kindness of Baron Von Karwinski, who twice measured this tree and has sent me a drawing of it, I am enabled to remove these doubts. The measurement was always taken above the dilatation, and on each occasion the size was found somewhat to exceed 117 feet. The dilated base was not measured, but from the drawing it must have a circumference of at least 200 feet, and thus the diameter of the trunk must be about 37·2 feet, and of the enlarged base about 60·5 feet. The dilated base surrounds the whole trunk equally, so that it cannot readily be supposed that the size is owing to the accretion of several trunks. Now if we take as a basis for computation the statement of Michaux, given by De Candolle, that the most thriving specimen of the tree in France attained in forty-five years a diameter of one foot or 144 lines, and consequently, that annual rings were formed of the thickness of 3·2 lines, and supposing a similar increase of wood to occur up to the most recent period of growth, it

would appear that the trunk in question, which has a diameter of 5352 lines, would be 1672 years old. This supposition, however, is rather improbable, since perhaps none of the Conifers in the later periods of their growth ever deposit so much as 12·8 lines of wood within four years. If again we assume the annual increase to average only one line, we get 5352 rings, and, consequently, that number of years is the age of the tree; but if we take the mean of these two numbers, we should arrive at 3512 as the most probable number of years of age, and at an annual addition of ligneous rings of 1·6 lines in thickness, which is sufficiently considerable. The uncertainty, however, of all such computations of age, taken from the measurement of the trunk, without actual counting of the rings, and the differences which in this respect are caused by climate and soil, may be seen from some examples.

"De Candolle considers the increase of diameter of the yew, at least in the first 150 years, to be about one line annually. In 120 years, consequently, a tree should be 120 lines, or ten inches thick. But four sections of the trunks of Taxus of various thickness have been measured in the mountains of Bavaria, and their annual rings counted with the following results:—

	Diameter.	Annual Rings.	Transverse Thickness of Rings.	
			In the diameter.	In the semi-diameter.
1.	56 lines	115	0·48 lines	0·24 lines
2.	69 lines	214	0·33 lines	0·16 lines
3.	132 lines	292	0·42 lines	0·21 lines
4.	132 lines	294	0·42 lines	0·21 lines

Thus the thickness of the annual rings amounts to only from one-fifth to nearly half a Bavarian line, a result which, if transferred to the large English specimens mentioned above, would double or treble their age. The thickness of the rings, however, was at the same time so various in the different individuals that in Nos. 1 and 2, thirteen lines of difference in the diameter corresponded to 99 annual rings; whilst in Nos. 2 and 3, sixty-three lines of difference

corresponded to only 78 rings; results which harmonise with the average thickness of the rings stated above, only inasmuch as that the individual rings of the same stem differ considerably among themselves. Four sections of Pinus sylvestris, taken from very different localities, were estimated in the same way.

	Locality.	Diameter.	No. of Annual Rings.	Thickness of Rings.	
1.	Place (unknown) . . .	50 lines	13	3·8 lines	1·10 lines
2.	About 5500 feet altitude, dwarf	72 lines	186	0·39 lines	0·19 lines
3.	About 5000 feet altitude, tall .	84 lines	154	0·54 lines	0·27 lines
4.	About 3500 feet altitude, tall .	84 lines	56	1·50 lines	0·75 lines

Thus in these four stems the thickness of the annual rings varied between 3·8 lines and 0·39 lines. At the same time, in Nos. 1 and 2, twenty-two lines of difference in diameter correspond with 173 annual rings, but between Nos. 3 and 4, and No. 2, the proportion is reversed, since in the two latter, a greater diameter corresponds with a less number of rings, for whilst in No. 4, the 84 lines of diameter correspond with 56 rings, in No. 2, seventy-two lines give more than three times that number, or 186 rings.

"Similar anomalies are presented by the Spruce Fir, Larch, and also by Pinus Cembra. These statements, however, suffice to prove that conclusions as to the age and number of annual rings of a tree cannot, at present, be drawn with any, or with only occasional, probability, from the diameter, except in those cases in which the growth has taken place under exactly similar external conditions. The four yew stems were from the Bavarian Alps, and the altitude of the respective localities at which they grew cannot differ more than 3000 feet; the thickness of the rings varies among them almost one-third; but in comparison with the instances given by De Candolle, more than the half or even two-thirds. According to this, yews of the same diameter may be 100, 200, or 300 years old. But in the Scotch fir the difference in the thickness of the rings, under great differences of external condition (as between Nos. 1 and 2) amounts to one-ninth; and under nearly similar circumstances (as

between Nos. 2 and 4) to at least a third, or (as between Nos. 1 and 4) to one-half.

"It would be a highly interesting contribution to science, if numerous comparative calculations and measurements were made in different countries, and under every variety of external conditions, for the accurate determination of the limits of this disparity in the growth of trees of the same species. The height of these trees has probably been exaggerated, when that of Araucaria imbricata has been stated to reach 260 feet, although 220 feet have also been given as that of Araucaria excelsa. In all the rest, the average height scarcely exceeds that of our Spruce and Silver Firs, which under very favourable circumstances will attain from 160 to 180 feet. The Scotch Fir (P. sylvestris) and Larch, with many others, though not of such lofty growth, nevertheless exceed 100 feet, and there are very few which do not reach 50 feet. The relative proportion of diameter to height varies extremely, as may be seen from these examples:—

	Height.	Diameter.	Proportion.
Araucaria excelsa . .	220	24	1 to 9
Abies excelsa . .	180	6	1 „ 30
Abies pectinata . .	180	7	1 „ 26
Abies larix . . .	120	12	1 „ 10
Taxodium distichum . .	120	36	1 „ 3·5
Taxus baccata . .	120	18	1 „ 7
Pinus bracteata . .	120	1	1 „ 120
Pinus sylvestris . .	130	6	1 „ 22

This table shows that the proportion between height and thickness varies from 1 : 3·5 to 1 : 120, and the difference with respect to dimensions which has been heretofore stated to exist between Monocotyledons and Dicotyledons cannot be maintained as regards this family. On the other hand, the trunk of the Cycas is frequently stunted to such a degree that its transverse diameter is almost equal to its length. The annual elongation is so small that scarcely any distinct internodes are observed between either the bud-scales or the fan-like tufts of leaves, and the whole surface of the stem appears closely imbricated with the remains of the dry scales and leaves. Exactly the same formation, with the exception of the texture of the wood, obtains in several of the Conifers, in

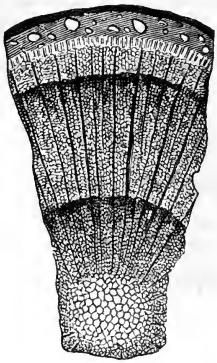
the lateral branches, where the afflux of the sap is diminished, and the longitudinal growth consequently reduced to the lowest possible degree, as, for instance, in the Larch, Cedar, Salisburia, &c. These stunted lateral branches, which are for the most part also fructiferous, present the greatest analogy in their formation with the stems of the Cycads." (*Ray Papers,* 1846, p. 21.)

To the characters above assigned to the stem of woody Exogenous plants there are some remarkable exceptions, caused by anomalous growth, and arising from a breaking up of the woody zones, or their fusion, or their separation by layers of cellular matter, or by the constant extension of their stem into angles, or by the formation in the same stem of several centres of growth instead of one. In all these cases it is interesting to observe that *the first growth is normal,* however anomalous it may afterwards become.

Mirbel has noticed the unusual structure of Calycanthus (*Annales des Sciences,* vol. xiv.), in the bark of which, at equal distances, are found four minute extremely excentrical woody axes, the principal diameter of which is inwards; that is to say, next the wood. The existence of this structure, noticed by the discoverer only in C. floridus, I have since ascertained in all the other species, and also in Chimonanthus. Gaudichaud attempts to explain this curious mode of growth upon the supposition that each leaf forms three fascicles of woody matter, whereof the central is the most powerful, and produces the mass of the stem; and the lateral ones, which are much weaker, give origin to the accessory axes;—and he states, that in climbing Sapindaceous plants the same phenomenon occurs, only to a far greater extent. He represents that in those cases the fibres of each leafstalk separate into three or four principal branches, each of which applies itself to one of the internal woody axes of the stem, which, in time, consists of from four to eight distinct axes, the central being larger than the others, and each having its own cortical integument. The fact is curious, (*Arch. de Bot.,* ii. 492.), and has been confirmed by Treviranus (*Ann. of Nat. History,* N. S. i. 126).

In Coniferous wood (*fig.* 35.) there is scarcely any mixture of bothrenchym among woody tissue, as in most other exogenous

fig. 35.



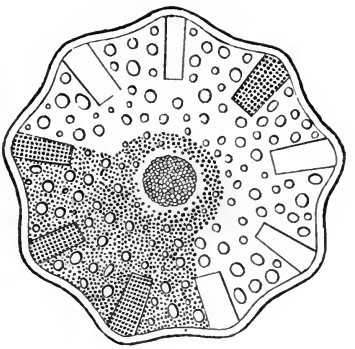
plants; in consequence of which a cross section exhibits none of those open mouths which give what is vulgarly called porosity to wood. Instead of this, the wood generally consists exclusively of that kind of tissue which has been described at p. 65, under the name of glandular, with the exception of the medullary sheath, in which spiral vessels are present in small numbers. The Yew and Abies Douglasii are the principal exceptions: in the former the woody tissue is the same as that of other Conifers; but many tubes have a great quantity of little fibres lying obliquely across them at nearly equal distances,—sometimes arranged with considerable regularity,—sometimes disturbed as it were,—so that the transverse fibres, although they retain their obliquity, are not parallel,—and sometimes, but more rarely, so regular as to give to the tubes of woody tissue the appearance of spiral vessels, the coils of which are separated by considerable intervals. The latter only is represented by Kieser, at his tab. xxi. fig. 103, 104.; but the former is by far the most common appearance.

In Cycads the vascular system is destitute of vessels, as in Conifers; their place being supplied by such bothrenchym as has been already described at p. 58. But the zones of wood are separated by a layer of cellular substance resembling that of the pith, and often as thick as the zones themselves,

while the pith itself is filled with bundles of fibro-vascular tissue. This structure is represented by Adolphe Brongniart, in the 16th volume of the *Annales des Sciences.*

Mr. Griffith has beautifully illustrated the structure of a plant called Phytocrene (*fig.* 36.), in Wallich's *Plantæ*

fig. 36.



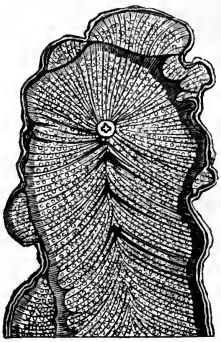
Asiaticæ, vol. iii. t. 216. In this curious production the wood consists of plates containing vessels and woody tissue, having no connection with each other, and separated at very considerable intervals by a large mass of prosenchymatous cellular tissue filled with vasiform tissue, and representing medullary rays. When the stem is dry, the woody plates separate from the other tissue, in which they finally lie loose.

In Nepenthes distillatoria the pith contains a great quantity of spiral vessels; the place of the medullary sheath is occupied by a deep and dense layer of woody tissue, in which no vessels, or scarcely any, are discoverable; there are no medullary rays; the wood has no concentric zones; between the bark and the wood is interposed a thick layer of cellular tissue, in which an immense quantity of very large spiral vessels is formed; on the outside of this layer, is a thinner coating of woody tissue, containing some very minute spiral vessels; and, finally, the whole is enclosed in a cellular integument, also containing spiral vessels of small size. In this singular plant

the outer layers are, it is to be presumed, liber and epidermis; and the cellular deposit between the former and the wood is analogous to cambium in an organised state belonging equally to the wood and the bark. What is so exceedingly remarkable is the complete intermixture of the vascular and cellular systems, so that limits no longer exist between the two.

I have a specimen of the twisted compressed stem of a Malpighiad from Columbia (*fig.* 37.), in which there are no concentric circles, properly so called; but in which there are

fig. 37.

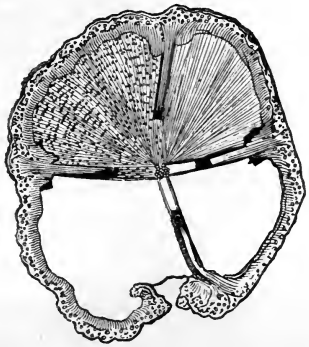


certain irregular wavy zones, consisting of a layer of cellular tissue coated by a stratum of woody tissue, enclosing, at irregular distances from the centre, very unequal portions of the vascular system. The pith is exceedingly excentrical; and the medullary rays, which are imperfectly formed, do not all radiate from the pith, but on the thickest side form curves passing from one side of the stem to the other, their concavities turned towards the pith.

In the stem of a Bignonia in my possession, from Colombia (*fig.* 38.), the vascular system is divided into four nearly equal parts, by four short thick plates radiating from the pith, and consisting of woody tissue, with a very few vessels. These plates are not more than one-third the depth of the wood; so that between their back and the bark there is a considerable vacancy, by which the four divisions of the

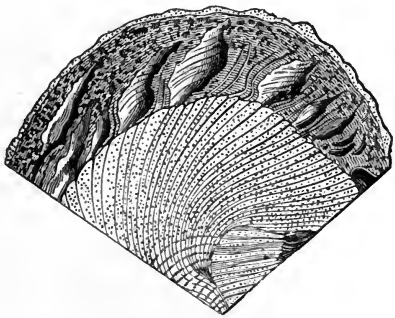
vascular system are separated. This vacancy is nearly filled with bark, which projects into the cavity.

fig. 38.



In Stauntonia latifolia, (*fig.* 39.), which has a twining stem, there are no concentric circles, and the medullary rays are curved, part from right to left, and part from left to right,

fig. 39.



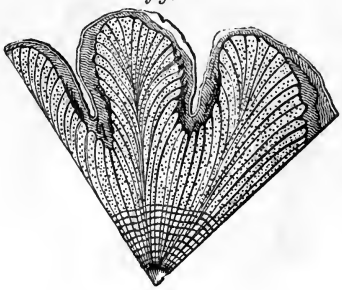
diverging at one point and converging at another: the bark is pierced with extensive longitudinal perforations.

In Euonymus tingens (*fig.* 40.), the vessels near the centre of the stem are arranged in concentric interrupted circles, but towards the bark there is no trace of such circles; the surface of the stem is deeply cut into lobes parallel with the stem, and the vessels are all confounded in an uniform mass.

Gaudichaud represents the stem of some Malpighiaceous

plants to be in like manner divided into a number of regular lobes, which however, actually reach the axis; and, in consequence of the twining habit of the stem, are twisted into the

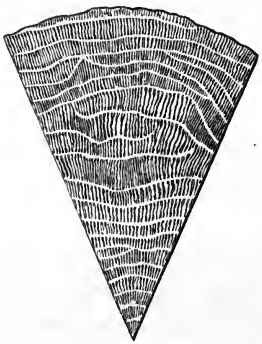
fig. 40.



appearance of a cable externally. In fact, the formation of longitudinal vertical plates or ribs (or, when old, buttresses) in Exogens, although unknown in Europe, is by no means of uncommon occurrence in tropical countries. The Ceiba Trees, (Bombax) are remarkable examples of it, their longitudinal projections extending far enough to conceal men in the angles, and Sir Robert Schomburgh found in Demerara a forest tree in which sections of even the young branches form a very regular five-armed Maltese cross.

In Cocculus laurifolius (*fig.* 41.) the concentric lines

fig. 41.

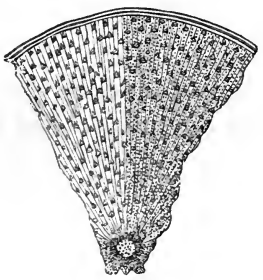


evidently belong to the medullary system; they are extremely interrupted and unequal, often only half encircling

the stem, or even less, and they anastomose in various ways; the medullary rays are unusually large, and lie across the wood like parallel bars; and, finally, the plates of which the wood consists each contains but one vessel, which is situated at the external edge of the plate.

None of the anomalous forms of Exogenous stems are, however, more remarkable than a Burmese Pisonia, (*fig.* 42.), for a specimen of which I am indebted to Dr. Wallich. In

fig. 42.



a section of this, the general appearance is so much that of an Endogenous stem, that without an attentive examination it might be actually mistaken for one. The diameter of this stem is two inches seven lines; it is nearly perfectly circular, and has a very thin but distinct bark, with a central pith surrounded by very compact woody tissue. There are neither zones nor medullary rays; but the vascular system consists of an uniform mass of vessels and woody tissue, disposed with great symmetry, and of the same degree of compactness at the circumference as in the centre. Amongst this wood are interspersed at the distance of about half a line, with great regularity, passages containing loose cellular tissue. These passages are convex at the back and rather concave in front, run parallel with the vessels, and do not seem to have any kind of communication with each other. They, no doubt, represent the medullary rays of the cellular system of this highly curious plant. It must be remarked, that the resemblance borne by this stem to that of an Endogenous plant is more apparent than real; for whilst, in the latter, the vascular

system is separated into bundles surrounded by the cellular system, in this, on the contrary, the cellular system consists of tubular passages, surrounded by masses of the vascular system.

A very remarkable peculiarity among the order of Loranths is described as follows by Dr. Joseph Hooker, in the Myzodendron brachystachyum. "A branch, after attaining the age of two years and upwards, consists principally of a soft white cellular tissue, occupying the axis of the plant, and communicating with the thick bark by means of broad medullary rays. The latter are separated by woody plates, disposed in two concentric series, and formed almost entirely of scalariform tissue with sometimes pleurenchyma. The cuticle is very stout in texture: in a first developed branch it consists of only one row of small cells; these must be rapidly added to, for after another year the cuticle of the same branch is of much greater density and formed of many series of cells, much blended together, though not so completely as to assume the appearance of a homogeneous tissue, without any trace of cellularity which it afterwards attains. The cuticle is devoid of stomata commonly so called, but furnished with numerous longitudinal prominences, each marked by a fissure. There is no actual stoma or communication between the external atmosphere and tissue of the bark, further than what may be supposed to be afforded by cellular tissue, which is a rapid conductor of moisture. These are very evident in the branches of the second year, no doubt answer to stomata, whether performing the same functions or no, and are an instance either of the cuticle retaining its originally cellular organisation at the point where they occur, or returning to that structure.

"The Bark is composed almost entirely of a mass of cellular tissue, shrinking much when the stem is dry. The epiphlœum is formed of several rows of transversely elongated thick-walled cells; it occasionally contains air-cavities, but these are not so numerous or conspicuous as in M. punctulatum. The vessels of the liber are disposed about half-way between the cuticle and wood, are often very inconspicuous and formed of scattered bundles of fibres, protected by very thick-walled

cells, as in most, if not all, the Loranthaceæ, at other times they are in two series or variously disposed. This tissue does not appear to pass from one internode to another, but to be interrupted at each articulation, as M. Decaisne found to be the case in Viscum. The parenchyma between the vessels of the liber and wood is often dense; sometimes, but rarely, these vessels are seen to be immediately in contact with the wood.

"Within the bark are arranged two concentric series of woody plates or wedges; these two series are separated by a zone of cellular substance, and are generally arranged with tolerable precision: besides these the pith of the plant is intruded upon by other wedges or bundles of vascular tissue, unsymmetrically disposed, one of them often occupying the axis itself. Each wedge or plate is composed principally of concentric layers of very large vasa scalariformia, becoming more densely packed and much smaller in diameter towards the axis of each layer, where they are almost invariably furnished with a spiral filament. Between the layers of the first three or five years there is generally deposited two bundles of pleurenchyma similar to that of the liber, one on each side, but between the more recent layers there intervenes only the more delicate vascular tissue as mentioned above; however, pleurenchyma is sometimes more copiously deposited between every layer. The narrow portion of each wedge invariably rests on a mass of pleurenchyma deposited at the same time as the fibres of the liber, that is during the first year, as in the common Miseltoe. The wedges of wood belonging to the second series are smaller than those of the first, but similarly formed in all respects, and consisting of as many layers, though the inner are very inconspicuous.

"The pith consists of cellular tissue similar to that of the liber, and is very lax even in the older stems.

"The transverse section of this stem appears at first sight to differ very remarkably from that of most exogenous plants; this arises from the wood being deposited in two concentric series, separated by a broad zone of parenchyma, from the great breadth of the medullary rays, the irregular distribution of the fibres of the liber which are sometimes biserial, and

the disproportionate amount of scalariform tissue. The structure of *M. punctulatum* (another species) is however far more abnormal, fibres of pleurenchyma being deposited in the axis of the stem, thus replacing the pith and forming very obsolete rays, and all future increment of the stem being affected by an addition of layers of variously marked scalariform tissue alone, as far as I have been able to observe.

"I shall next describe the course the vascular tissue pursues in the newly formed buds and branches, and thus attempt to explain the origin of the two series of woody plates which this species and M. quadriflorum DC. possess. A transverse section of the stem of a flower or leaf-bud made in the first year of its formation, presents a mass of globular utricles, covered with a delicate cuticle formed of one moniliform row of cells, and traversed by one series of twenty or thirty vascular bundles. These bundles descend from the base of each leaf, traverse the branch and enter the stem. A transverse section of the stem again, from which the bud or branch is given off, and below the point of attachment of the latter, presents two concentric series of vascular bundles, besides an imperfect third consisting of a few scattered promiscuously in the axis of the stem; the outer series was formed in the former, the inner is derived from the buds and branches of the present year.

"A longitudinal section through the axis of the stem, so made as to pass also through the axis of the branch, clearly shows that it is due to the position in which the buds are developed, that a second series of wedges of wood is deposited. The buds originate towards the axis of the stem, within the vascular bundles of the previous year, and opposite the insertion of the petiole. The whole of the vascular tissue descending from a bud is consequently deposited within the wood of the former year; generally each bundle on entering the stem from the branch divides, one portion joining the old wood; the other, remaining free, and descending the stem, forms the second or inner plate of wood. The course of the bundles is, however, very uncertain; sometimes they do not divide, but either join the old vascular tissue, or continue free, and at others one portion crosses to the opposite side of the stem.

"As each bud gives off thirty or forty bundles of vessels, and these being superadded to those of the branch, such a plexus arises at the contracted junction of the second year's branch, and that of the third year, that their course can no longer be followed. Each of the woody plates, however, continues to receive accessions throughout the life of the plant, those of the inner series containing as many layers as those of the outer. It is hence evident that the bundles first arranged in the branch of the second year, on entering that of the third year, must present a very complicated arrangement of tissues. The increase of the stems in diameter being, however, effected throughout the length of the plant by an addition of matter to the outside of both concentric series of wedges, it follows that the growth is in one sense at the same time Exogenous and Endogenous.

"However complicated the nature and disposition of these tissues may cause the development of the stems to appear, the order in which each wedge of wood and its layers of pleurenchyma are deposited in the first year is the same in Viscum; nor are the tissues themselves very different from those of that plant." (*Flora Antarctica*, i. 298, with numerous well-executed figures of the anatomy.)

Among herbaceous stems that of Lathræa, which has been carefully studied by M. Duchartre, may be taken as a good example of anomalous organisation. In the stem of this plant he finds, as in all the stems of Dicotyledons, the pith, the ligneous system and the cortical system formed of the liber and of the cellular envelope; but he noticed two characters which appear to remove this plant from the usual structure of these vegetables. The first consists in the absence of a medullary sheath, that is to say, of a first interior zone of vessels of a different nature to those of the ligneous zone, and comprised between the pith and this ligneous zone. It is these vessels which, in the ordinary Dicotyledons, belong to the form designated by the name of true spiral vessels or of unrollable spiral vessels, and it is in this position alone that these vessels are found in the stem. Here nothing similar occurs; the vessels nearest to the pith consist of finely reticulated vessels, similar, although finer, to those

which exist in the rest of the ligneous layer. There are no tracheæ with a continuous free and unrollable spiral fibre. This character, however, although forming an exception to the most usual organisation of dicotyledonous plants, is met with in other vegetables of this class, and particularly in most parasitical plants, although the unprecise manner in which authors apply the word spiral vessels may sometimes leave a doubt on this point. A second remarkable character of the ligneous body of this plant consists in the complete absence of medullary rays. This fact is well established by M. Duchartre, and is placed beyond all doubt. The ligneous zone is entirely formed of cells elongated in the longitudinal direction of the stem, and consequently parallel to the pith, intermixed with more or less finely reticulated vessels, and thus appearing most frequently radiated or punctated; it is not interrupted at any point by those lines of cells in a radiating direction, which, extending from the pith toward the bark, constitute the medullary rays. An analogous structure had been already noticed by M. Brongniart in a family very far removed from the Lathræa, in the Crassulaceæ, in which the ligneous zone is equally unfurnished with medullary rays, and is only constituted of tissues elongated in the direction of the axis and perfectly continuous. Having desired to ascertain whether, in the family to which the Lathræa clandestina belongs, this character was found in any other plant, it was found that the Melampyrum sylvaticum presented the same continuity in the elongated tissues of the ligneous zone, and that there was also a complete absence of medullary rays. It thus appears that there exists in several Dicotyledons an organisation of the stem which botanists were far from suspecting some years ago, and which deserves the attention of physiologists. (See the translation of Duchartre's paper in the *Annals of Natural History*, vol. xv.)

A great number of similar anomalies have now become known to botanists, and will be found recorded, and sometimes figured, in the works of Decaisne, Adrien de Jussieu, Ach. Richard, Gaudichaud and others, and in the Penny Cyclopædia. They occur more especially among Soapworts (Sapindaceæ) Chenopods, Nyctagos and Loranths; some of them

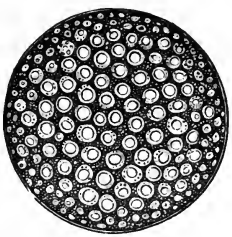
will be referred to hereafter in the explanation to be given of Schleiden's peculiar views of the structure of stems. Without plates it would be of little use to introduce these descriptions, nor, in the absence of some good theory, which will connect such examples with some general law, does it appear necessary to the purposes of the student that they should be particularised.

§ 2. *Of the* Endogenous *Structure.*

fig. 43.

Plants of an arborescent habit having this structure being almost exclusively extra-European, and most of them natives only of the tropics, botanists have had much fewer

fig. 44.



opportunities of examining them, and, consequently, our knowledge concerning them is more limited. Nevertheless,

the investigations of Mohl and others have thrown great light upon their real organisation.

In Endogenous plants the vascular and cellular systems are as distinct as in Exogenous, but they are differently arranged. The cellular system, instead of being distinguishable into pith, bark, and medullary rays, is a uniform mass, in which the vascular system lies imbedded in the form of thick fibres, seldom having any tendency to collect into zones or wedges resembling wood. The fibrous bundles consist of woody tissue, enclosing spiral or other vessels.

The following is an explanation of the opinions generally entertained concerning the formation of an Endogenous stem. Its diameter is supposed to be increased by the constant addition of woody bundles to the centre, whence the name; those bundles displace such as are previously formed, pushing them outwards; so that the centre, being always most newly formed, is the softest; and the outside, being older, and being gradually rendered more and more compact by the pressure exercised upon the bundles lying next it by those forming in the centre, is the hardest. In Endogenous plants that attain a considerable age, such as many Palms, this operation goes on till the outside becomes sometimes hard enough to resist the blow of a hatchet. It does not, however, appear that each successive bundle of fibres passes exactly down the centre, or that there is even much regularity in the manner in which they are arranged in that part; it is only certain that it is about their centre that they descend, and that on the outside, below the growing point, no new formation takes place from the circumference. This appears from the manner in which the bundles cross and interlace one another, as is shown in the figure of Pandanus odoratissimus given by De Candolle in his *Organographie* (tab. vi.), or still more clearly in the lax tissue of the inside of the stems of Dracæna Draco.

The investigations of Mohl appear, however, to prove that this view of the structure of Endogens requires some modification. According to this observer, every one of the woody bundles of a Palm stem originates in the leaves, and is at first directed towards the centre; arrived there, it follows the

course of the stem for some distance, and then turns outward again, finally losing itself in the cortical integument. In the course of their downward descent, the woody bundles gradually separate into threads, till at last the vascular system, which for a long time formed an essential part of each of them, disappears, and there is nothing left but woody tissue. In this view of the growth of Endogens, the trunk of such plants must consist of a series of arcs directed from above inwards, and then from within outwards; and consequently the woody bundles of such plants, instead of being parallel with each other, must perpetually intersect each other. If Mohl's view of the structure of Endogens be correct, they must after a time lose the power of growing, in consequence of the whole of the lower part of their stems being choked up by the multitude of descending woody bundles. The lower part of their bark, too, must be much harder, that is, much more filled with woody bundles, than the upper. The hardness of the exterior of Palm stems cannot be owing to the pressure of new matter from within outwards, but to some cause analogous to the formation of heartwood in Exogens. Is there any proof that such a cause is in operation? These inquiries have been partially answered by Mr. George Gardner, from observations made by him in Brazil. He made a vertical section of a Palm Tree four inches in circumference, and he was able plainly to trace woody bundles proceeding from the base of the leaves to the centre of the stem, at an angle of 18°; they then turned downwards and outwards to within a few lines of the external cortical part of the stem, running parallel with its axis. The distance between the ends of the arcs was about two and a half feet. He adds, that the wood of Palm Trees is much harder at the bottom than in any other part of the stem, the inhabitants of tropical climates using only this part for economical purposes. (*Taylor's Magazine*, xi. 553.)

The epidermis of an Endogenous stem seems capable of very little distension. In many plants of this kind the diameter of the stem is the same, or not very widely different, at the period when it is first formed, and when it has arrived at its greatest age: Palms are, in particular, an instance of

this; whence the cylindrical form that is so common in them. That the increase in their diameter is really inconsiderable, is proved in a curious, and at the same time very conclusive, manner, by the circumstance of gigantic woody climbing plants sometimes coiling round such stems, and retaining them in their embrace for many years, without the stem thus tightly wound round indicating in the slightest manner, by swelling or otherwise, that such ligatures inconvenience it. A specimen illustrative of this is preserved in the Museum of Natural History at Paris, and has been figured, both by Mirbel in his *Elémens* (tab. xix.), and De Candolle in his *Organographie* (tab. iv.). We know from the effect of the common Bindweed upon the Exogens of our hedges, that the embrace of a twining plant is, in a single year, destructive of the life of every thing that increases in diameter; or at least produces, above the strangled part, extensive swellings, which end in death. Some Palm Trees, however, bulge out in the middle, and then contract again to their previous diameter.

It is, also, certain that other Endogens do increase extensively in diameter up to a certain point; sometimes this is effected with great rapidity; and the horizontal growth once stopped appears never to be renewed: thus in the Bamboo, stems are sometimes found as much as two feet in circumference, which were originally not more than half an inch in diameter. Others would seem to have an unlimited power of distension: in the Dracænas, called in the French colonies in Africa Bois-chandelles, the first shoot from the ground is a turio (sucker), an inch in diameter; and perhaps fifteen feet high; but in time it distends so much that sometimes two men can scarcely embrace it in their extended arms. (*Thouars, Essais,* p. 3.)

As Endogenous stems contain no concentric zones, there is nothing in their internal structure to indicate their age; but in the opinion of some botanists, there are sometimes external characters which will afford sufficient evidence of it. It is said that the number of external rings which indicate the fall of leaves from the trunk of Palm Trees coincides with the number of years that the individual has lived. There is, however no proof of this at present; such statements must, therefore,

be received with caution. It may further be remarked, with reference to this subject, that in many Palms these rings disappear after a certain number of years.

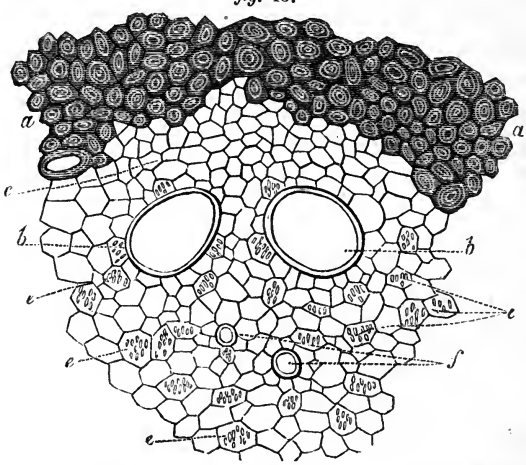
In arborescent Endogens it usually happens that only one terminal leaf-bud developes; and in such cases the stem is cylindrical, or very nearly so, as in Palms. If two terminal leaf-buds constantly develope, the stem becomes dichotomous, but the branches are all cylindrical, as in Pandanus and the Doom Palms of Egypt; but if axillary leaf-buds are regularly developed, as in the Asparagus, Dracæna Draco, or in arborescent grasses, then the conical form which prevails in Exogens exists in Endogens also.

In Endogens there are but few important anomalies in structure; and of these the most striking, namely that of Grasses, is more peculiar than anomalous. Yucca appears, from a figure of Meneghini (*Ricerche sulla Struttura del Caule nelle Piante Monocotyledoni*, t. ix. f. 1. c.), to arrange its woody bundles in concentric layers when old; Smilax has a stem strictly endogenous, and a root which approaches in structure the stem (not root) of Exogens; and, in the article Endogens, in the Penny Cyclopædia, I have shown that the stem of Barbacenia is composed of roots of an endogenous nature, held together by the adhesion of their cortical integument, and that of a very slender central true stem on which they are moulded. In Grasses the stem is hollow except at the nodes, where transverse partitions intercept the cavity, dividing it into many cells. In the Bamboo these cells and partitions are so large that, as is well known, lengths of that plant are used as cases to contain papers. But if the gradual development of a grass be attentively observed, it will be found that the stem is originally solid; that it becomes hollow in consequence of its increasing in diameter more rapidly than new tissue can be formed; so that its deviation from the ordinary characters of Endogenous structure is much less considerable than it seems to be at first sight.

According to Mohl, the structure of an Exogenous and an Endogenous stem, during the first year of their growth, is altogether the same; but in the second year the wood and the liber of the former separate, and new matter is then

interposed, while, on the contrary, in Endogens no such separation occurs, and consequently the newly-formed matter of the stem is forced towards the centre, through which it passes, with a constant tendency, however, to reach the outside. I confess, I do not perceive this analogy; on the contrary, if we compare the new shoot of an Asparagus and that of an Elder-bush, the difference between them will be too great to be thus explained away. M. Dutrochet thinks that in the globular rhizome of Tamus an argument may be found to show the identity of Exogens and Endogens *in* the first period of their growth; but if this were admitted, it is equally evident, from the same example, that they become entirely different immediately *after* the first period. Nor, indeed, is the anatomy of the woody tissue, which constitutes the ligneous wedges of Exogens, the same as that which forms the woody bundles of Endogens. In the latter each woody bundle is, when divided transversely, described by Mohl as consisting of the following parts (*fig.* 45.) :—

fig. 45.



a Thick-sided woody tissue (*cellulæ libri*).
b Bothrenchym (*vasa porosa*).
c Thin-sided parenchym (*vasa propria*).
e A variety of bothrenchymatous tissue (*cellulæ ligni punctatæ*).
f Spiral vessels.

But this is quite unlike the anatomy of the smaller portions

of woody tissue in Exogens, in which there is no such arrangement of woody tissue, so called vasa propria, or spiral vessels.

Very accurate and elaborate inquiries into the structure and development of Endogens have been instituted by Mirbel, who does not admit that the woody bundles proceed from the leaves; but believes that he has proved their origin to be independent, in the growing point, or *phyllophore*, as he terms it, whence they lengthen upwards, introducing themselves into the leaf,—and downwards, passing through the medullary matter of the stem. Von Martius gives the following as his latest opinion of the true structure of Palms, after a consideration of all the evidence that had been collected in April, 1845:—

1. The stem of Palms does not contain more woody bundles than are destined to enter sooner or later into the leaves.

2. The woody bundles originate on the summit of the stem, in the growing point or phyllophore of Mirbel, between the new and plastic parenchyma which there forms a peculiar conical layer, covering, like a funnel, the more aged parts. They are always external with relation to those which are already formed, and a little higher.

3. The points of origin of the woody bundles are organically predetermined; we find, in these points, the fibres situated obliquely, and converging at their upper ends. They lengthen from both ends—that is to say, they grow from below upwards, and from above downwards.

4. The upper extremity of these woody bundles is directed towards the base of the young leaf; the latter originates in the form of a cellular fold in the centre of the bud, and is directed towards the circumference on becoming enlarged.

5. The lower extremity is extended obliquely downwards, and terminates, in the form of an extremely slender and mere parenchymatous filament, upon a layer at the circumference. This layer is wholly different from the liber of Dicotyledons in development; it may, however, be compared to that part of their system as regards its constituent elements.

6. The spot where the upper extremity of the woody bundle enters the leaf, is either on the same side of the stem by which it passes downwards, or on the side exactly opposite. In this second case the woody bundle passes quite through the stem.

7. The woody bundles necessarily decussate; some in the central part of the stem, others by bending suddenly to enter a leaf on the side where they originate.

8. Growth is effected in a solid organic mass, between the formation of the elementary organs, and the manner in which leaves are arranged. It is especially their position and the succession of the systems of phyllotaxis (which generally increase by specific complications in each species of Palm), that we must regard as the conditions of the modifications in the decurrence of the fibres and the formation of the wood.

9. The oldest part of the woody bundles is not at either their upper or lower extremity; they are most completely developed in the middle of their downward growth. At the lower end they consist only of parenchymatous cells; at their upper extremity they are divided into several finer vessels which enter the leaves.

10. The lower extremity does not extend to the roots; it does not go beyond the column, where the organic separation of the descending and ascending axis occurs.

11. The stem becomes more woody and harder by the growth of the ascending and decussating woody bundles; the parenchym between the woody bundles also becomes thicker and harder. This hardening bears a direct relation to the age of the tree; and as the elements of organisation which are first formed are collected at the circumference, the stem is necessarily harder in that part. (*Comptes rendus*, 1845, April 7.)

Endogens have no bark. They have a cortical integument composed of an epiphlœum and an inner layer, analogous, perhaps, to liber; and the woody part of which, according to Mohl, is formed in Palms by the introduction of the ends of the woody arcs of the stem. In Tamus elephantipes the epiphlœum acquires the nature of cork, but splits into

pyramidal laminated areæ. This approximates the cortical integument of Endogens very little to true bark, which is essentially characterised by being separable from the wood; and having its woody tissue parallel with that of the stem, and formed altogether in an independent, though parallel direction. The apparent bark of Endogens is, in fact, analogous to the mesophlœum and epiphlœum, or cortical integument of Exogens.

Schleiden's Theory of Stem Formation.

The views of this Botanist are so peculiar that they demand a separate place. I accordingly give the substance of his theory, from his paper *Uber die Anatomisch-physiologischen Verschiedenheiten der Stengelgebilde,* published in Wiegman's Archiv. for 1839, p. 219. Schleiden expresses his surprise that among the numerous controversies which have arisen as to the differences between monocotyledonous and dicotyledonous stems, comparisons should be generally confined to the so-called woody trunks of Palms, and those of the common dicotyledonous forest trees of Europe, botanists having, in doing thus, brought into comparison things which are wholly dissimilar. A Palm-stem originates from undeveloped interfoliar organs; but dicotyledonous woody stems from fully developed parts; a distinction of such importance in plants furnished with numerous series of woody bundles, that the stalk of a pink, and the culm of a grass, do not differ so much as the latter and the axis of a bulb.

The following differences usually occur in stems, and depend upon various modes of the development, arrangement, and structure of woody bundles.

I. The woody bundles always grow from the interior to the exterior, and are either LIMITED or UNLIMITED in their growth. In general every woody bundle consists of three parts, having a different physiological value, of very delicate tissue, rapidly formed and of most tender texture, in which new cells are continually generated, and deposited in various ways; some directed towards the exterior, in the shape of a peculiar tissue having long very thick-walled cells, (liber,) and others towards the interior, in gradual succession, in the

form of annular, spiral, reticulated, or porous tubes, and ligneous cells; the latter, whether uniform or different, forming the wood, properly so called. Up to a certain period the development of the woody bundles proceeds in the same manner in both Monocotyledons and Dicotyledons; but after a time, in Monocotyledons, the fast-growing, thin-walled cellular tissue suddenly changes, the partitions of its cells become thicker, their power of producing fresh cells ceases, and, as soon as all the surrounding cells are fully grown, a new and peculiar form is assumed, and gum, mucilage, &c., or other dense organisable matter ceases to be conveyed. At the time when the development of these cells ceases, they are called by Mohl *vasa propria*. Owing to the circumstance just explained all further development of these woody bundles is rendered impossible, and, therefore, I call them LIMITED (*geschlossen.*) In Dicotyledons, on the contrary, this tissue, which is in such plants termed *cambium*, by authors, or *couche régénératrice*, by Mirbel, retains its vital power during the whole life of the plant, continuing to generate new cells, which thus increase the mass as they go on, adding partly to the exterior, (liber,) and partly to the interior, (wood,) for an indefinite time. This takes place according to the climate and nature of a plant, either with little interruption, as in the Indian Figs, (Cactaceæ,) or periodically, rapid formation alternating with almost entire cessation of growth, as in our forest trees. In the latter, a little perseverance and delicate manipulation proves, that the stem forms a continuous tissue, from the pith to the bark, at all periods of its life, and that the bark never really separates from the stem; what has been called a separation being in fact a mere rending asunder of the delicate tissue called cambium, which is really present, even during winter, and thus lays the foundation of a new annual zone, although it is compressed, and filled with gum, starch, or other substances. In the spring, it is expanded and swollen by the current of new sap, and its contents are dissolved out. In all cases it may be shown conclusively that the new cellular tissue is always formed within that already existing, that is to say, in primitive cells, by means of cytoblasts, in the

same manner as in other cells. In fact young cells are constantly formed in either the upper or lower end of the long original cells (pleurenchym,) and in consequence of their extension grow through them, when, coming in contact with the other end of the cell, they seem to call into existence a new cell at the corresponding place in the cell which immediately follows. In this difference between limited and unlimited woody bundles consists the only universal distinction between Monocotyledons and Dicotyledons. In annual Dicotyledons the woody bundle, checked in its further development by the death of the plant, has, it is true, some similarity to Monocotyledons; nevertheless the difference may with care be distinctly perceived, for the formative layer always retains to the last its generating power; and upon this property is, in fact, founded the lignification of certain annual plants, when they are not allowed to flower, as happens in Mignonette and Stocks.

II. A second distinction among stems, is founded on the number and arrangement of these woody bundles, that is to say upon whether only a simple circle, or several are present. In the first case the woody bundles generally approach each other sooner or later, and thus form a hollow cylinder, pierced from within outwards by bands of compressed parenchyma, called medullary rays. But this closing up does not always occur in annual stems, and consequently, there is no difference, except in the nature of the vessels, between the woody skeleton of Tropœolum majus (consisting of unlimited woody bundles), and the creeping stem of Polypodium ramosum (consisting of limited woody bundles). It is only when a well-defined limit is produced by the closing up of a single circle of woody bundles, that there can be a question about bark and pith. In the beginning nothing is present in a stem except uniform parenchym, and it is only after a part of this has grown into woody bundles, that a difference can be found between the central substance (pith) and the external substance (bark); the medullary rays, which may be traced through all gradations, from narrow plates to a continuous parenchymatous mass, traversed by some thread-like woody bundles, still preserving the connexion. Hence the dispute

about bark, or no bark in Monocotyledons, is either an idle quarrel about words, or is grounded on something decidedly false. It is, however, to be borne in mind, that what many have called the bark of Monocotyledons, is very different in its origin, structure, and physiological importance, from the bark of the Dicotyledons.

A simple closed-up circle of woody bundles only occurs, so far as I know, in the stems of Dicotyledons. In Monocotyledons, on the contrary, I believe, it regularly occurs in the roots.

The case of many circles of woody bundles, occurs throughout Monocotyledons, and is to be found among Dicotyledons, in Pepperworts (Piperaceæ), Nyctagos, Amaranths, Chenopods, and perhaps many others, the structure of whose stems is at present ill known. Meanwhile, the great distinction of Monocotyledons, namely their limited woody bundles, here comes into play, for the unlimited bundles of the above-named Dicotyledons give rise to a very peculiar woody structure. Dr. Robert Brown first drew my attention to this in the stem of the Pisonia, (figured in Lindley's *Introduction to Botany*, fig. 42.) There the woody bundles, arranged in various circles, continue to develope until at last they almost form a continuous mass; hence the parenchym, which previously separated them, is compressed into small insulated patches, which, when the wood is completely formed, are scattered through it in narrow vertical cords (*stränge*), which may be termed, not incorrectly, vertical medullary rays. On the outside of these cords, on the wood, are frequently found spiroids still unaltered and forming the commencements of outer woody bundles. I have traced the whole development of this singular structure in two species of Pisonia, in Amaranthus viridis, Beta Cicla, Atriplex hortensis, Chenopodium Quinoa, &c. The structure of many others of the same families, especially Pepperworts, although imperfectly examined by me, proves that this peculiarity is general among them.

There is a curious kind of wood, which, with perhaps the whole family of Houseleeks (Crassulaceæ), seems to be constructed upon the same plan. In the old stem of an Echeveria

I found a uniform mass of wood, formed of prosenchymatous cells without vessels, among which are scattered small vertical cords of a very delicate parenchym, in the midst of which ran spiral vessels, most of which could be unrolled.

III. A third matter of importance, arising out of such essential differences in the stem, is the relation of the axis to leaves and buds, with which are connected many striking appearances.

a. A phenomenon common to all Dicotyledons, is the formation of nodes. The lateral organs (appendages of the axis), in fact, never originate among Dicotyledons at any other place than the nodes, where we find a peculiar arrangement of the vascular system which may always be ascertained by careful dissection. At such nodes there appear two or more woody bundles which, by being merely placed one on the other, or by anastomosing, form a loop (*ansa*) and from this plexus the organs of the circumference derive their woody bundles. From this, in connexion with the peculiar form of the medullary rays, arises an infinite variety of woody structure. This loop is more especially intended to connect the parenchym of the lateral organs with the pith or living parenchym of the axis. The size of the loop is essentially dependent on the thickness of the base of the leaves or lateral buds.

In Monocotyledons, this formation of nodes is rare, if indeed it occurs at all; for I am not sure that a real anastomosis of the vascular system occurs in the so-called nodes of grasses, for the purpose of giving off woody bundles to the lateral organs. This, at least, is certain, that in Monocotyledons the anastomosis of the vascular system is undoubtedly more rare than in Dicotyledons. If we could be sure that the formation of true nodes did not occur amongst Monocotyledons, we should have a fundamental distinction between them and Dicotyledons.

In Acotyledons we again find a true dicotyledonous formation, and much needless discussion about the peculiarities in the stems of Ferns would have been spared, if the plan of structure from which it is said to deviate, (viz., the dicotyledonous stem) had not been limited

by the study of an Oak or Lime Tree, but had been extended to various types of other families. I believe it would not be difficult for me to prove that all the modifications of woody tissue in ferns occur in every essential point among Spurgeworts (Euphorbiaceæ) or Indian Figs (Cactaceæ).

b. Whenever woody bundles pass off into an organ on the circumference, they must decussate with the parts which are formed afterwards, and on the outside of the point of departure. This is self-evident, and, so far from being a peculiarity of growth in Monocotyledons, it alone might have led to the conclusion that what is called Endogeneity has no existence. But it is most strikingly apparent in the separate limited woody bundles of Monocotyledons; although well enough in other cases, as for instance in old Melocacti, Echinocacti, and Mammillariæ.

c. But the most important circumstance of all must be taken to be whether the interfoliar parts are developed longitudinally or otherwise. In the first case, all the new parts originate upon the surface, (whether they are new woody bundles or an extended development of old ones), and add to the thickness of the stem, without its length being increased by these additions. It is otherwise when the interfoliar parts are undeveloped. In such cases, my observations show that from the period of germination, or the formation of a node, the force of growth not being able to take effect lengthwise, widens each succeeding internode more and more until a certain period, so that every internode projects somewhat beyond that which preceded it, and thus the original lateral surface is converted into a lower surface. A good example of this, is the development of bulbs, and of Melocacti. This increase in size of the internodes goes on only until the plant has formed a sufficiently broad basis. Afterwards, the new internodes cease to expand beyond the old ones; and a stem appears gradually increasing in height, but not in thickness, the interfoliar parts, successively added to each other, resembling hollow cones. A renewal of gradual expansion of the inter-

nodes occurs as an exceptional case in those Palm-stems which are swollen in the middle. Those who would study this form of stem in Monocotyledons and have not Palms at hand, may take Allium strictum and senescens, &c., which are in reality, Palm-stems in miniature.

IV. Other varieties of dicotyledonous structure result from the excessive enlargement (*hypertrophy*) of the pith, or bark, or both, as in Spurges, (Euphorbiæ,) Indian Figs (Cactaceæ), many tubers, as the Potato, and particularly in Cycads, whose stem has only a superficial resemblance to that of Palms, and is much more nearly allied to that of Fern-stems, differing, however, essentially in its unlimited woody bundles, and approaching far more to Indian Figs.

V. Finally, the nature of the cells which compose the woody bundles, either originally or eventually, differs much more than has been hitherto believed. The light wood of Avicennias consists almost wholly of porous tissue. The light and soft wood of Bombax pentandrum, of parenchym, spiral, annular, and reticulated vessels; but rarely of prosenchym, in the outside of its annual rings. The wood of the Melocacti, Mammillariæ and Echinocacti consists entirely of short, broad, thin-walled cells, terminating above and below in an obtuse cone, and having very thick rings or spires attached by their narrow edge, like those which Meyen has represented in his *Phytotomie*, from Opuntia cylindrica, where they occur, as in most of the Opuntiæ, though in less abundance, at the contractions of the joints. It is well known that in Conifers and Cycads the cells which form the wood are all alike, and do not consist as in many other kinds of wood, of prosenchym, and vessels. In many plants the first formed spiral vessels of the medullary sheath become changed by their great extension in length, into annular vessels, in which form they are left; in other plants the spiral vessels do not show this tendency, notwithstanding the great extension they undergo; in such cases they are frequently lengthened to such a degree as to resemble a mere thread lying in an intercellular passage, and they are frequently entirely re-absorbed. This may be beautifully observed in Opuntia monacantha, cylindrica, Mammillaria

simplex, Helleborus fœtidus, &c. Perhaps this is the reason why we, in many cases, find no genuine spiral vessels in the developed stem, even in the medullary sheath.

The study of the structure of stems is a boundless field for research. Up to the present time no one has given a correct explanation of that curious formation among the natural order of Soapworts, (Sapindaceæ,) where in the same stem we have several centres of wood-formation, only one of which occupies the axis. Nor is much that can be called satisfactory known of the real structure of the stem of Phytocrene, or of the analogous forms frequently occurring among Bignoniads.

While I give all possible credit to Dr. Schleiden for the ingenuity and originality of these views, I cannot say that I see how they affect the distinction stated to exist between Exogens and Endogens, or offer any valid objection to the employment of those terms.

SECT. III.—*Of the Root, or Descending Axis.*

At or about the same time that the ascending axis seeks the light and becomes a stem, does the opposite extremity of the seed or bud bury itself in the earth and become a root, with a tendency downwards so powerful, that no known force is sufficient to overcome it. It is invariably an extension of the longitudinal, or fibrovascular system, except when it is first born in the embryo. When put forth by stems a branch of fibrovascular matter is thrown off, pierces the superincumbent cellular tissue in part, and in part pushes it before it as a covering, or causes it to be generated in consequence of some specific action exercised by the young root.

As there are latent buds, so are there latent roots. This is positively asserted by M. Trécul, who has paid much attention to the subject, and must be evident enough to any one who ever examined a branch of the common Laurel (Cerasus Laurocerasus), grown in a damp and shady place, and injured by any circumstance. In such a case swarms of latent roots spring up, and actually force back the bark.

Independently of its origin, the root is to be distinguished from the stem by many absolute characters. In the first

place, its ramifications occur irregularly, and not with a symmetrical arrangement: they do not, like branches, proceed from certain fixed points (buds), but are produced from all and any points of the surface. Secondly, a root has no leaf-buds, unless, indeed, as sometimes happens, it has the power of forming adventitious ones; but, in such a case, the irregular manner in which they are produced is sufficient evidence of their nature.* Thirdly, roots have no scales, leaves, or other appendages; neither do they ever indicate upon their surface, by means of scars, any trace of such: all underground bodies upon which scales have been found are stems, whatever they may have been called. A fourth distinction between roots and stems is, that the former have never any stomates upon their epidermis; and, finally, in Exogens the root has usually no pith. It has been also said that roots are always colourless, while stems are always coloured; but aërial roots are often green, underground stems are colourless; and many true roots are deeply coloured, as in the Beet and Rhubarb.

The body of the root is sometimes called the *caudex;* the minute subdivisions have been sometimes called *radicles,*—a term that should be confined to the root in the embryo; others name them *fibrils,*—a term more generally adopted; while the terms *rhizina* and *rhizula* have been given by Link to the young roots of mosses and lichens.

A *fibril* is a little bundle of bothrenchym, or sometimes of spiral vessels, encased in woody fibre, and covered by a lax

* In general the roots of plants are, under natural circumstances, destitute of this power; and instances to the contrary are regarded as curious exceptions to a common law. Such exceptions are found in the Moutan Pæony, in the Plum tree, the Cydonia japonica, and others; but in none of them, nor in any other species with which I am acquainted, does the power reside in the same degree as in the Japan Anemone (*Anemone japonica*). If a root of this plant be taken from the ground after flowering, it will be found to resemble brown cord divided into a vast number of ramifications. Upon its surface will be perceived a great multitude of little white conical projections, sometimes growing singly, sometimes springing up in clusters, and occasionally producing small scales upon their sides. They are young buds, every one of which, if cut from its parent, will grow and form a strong young plant in a few weeks. These buds are not confined to the main trunk of the root, but extend even towards its extremities; so that every fragment of the plant is reproductive. (See *Gardeners' Chronicle*, Jan. 1, 1848, for a figure of this structure).

cortical integument: it is in direct communication with the vascular system of the root, of which it is, in fact, only a subdivision; and its apex consists of extremely lax cellular tissue and mucus. This apex has the property of absorbing fluid with great force, and has been called by De Candolle the *Spongiole* or *Spongelet*. It must not be considered a particular organ; it is only the newly formed and forming tender tissue. In Pandanus the spongelets of the aërial roots consist of numerous very thin exfoliations of the epiphlœum, which form a sort of cup, apparently intended for holding water for the supply of the roots.

The proportion borne by the root to the branches is extremely variable: in some plants it is nearly equal to them, in others, as in Lucerne, the roots are many times larger and longer than the stems; in all succulent plants and in Cucurbits they are much smaller. When the root is divided into a multitude of branches and fibres, it is called *fibrous:* if the fibres have occasionally dilatations at short intervals, they are called *nodulose*. When the main root perishes at the extremity, it receives the name of *præmorse*, or *bitten* off: frequently it consists of one fleshy elongated centre tapering to the extremity, when it is termed *fusiform* (or *tap-rooted* by the English, and *pivotante* by the French): if it is terminated by several distinct buds, as in some herbaceous plants, it is called *many-headed* (*multiceps*). The turnip has been occasionally referred to a root. But, from the investigations of Turpin and others, there is no room to doubt that the turnip, the radish, the cyclamen, and the elephant-foot, are all distensions of the stem: either of the first internode, or of the inferior prolongation of the stem below the cotyledons and above the root.

The roots of many plants are often fleshy, and composed of lobes, which appear to serve as reservoirs of nutriment to the fibrils that accompany them; as in many terrestrial Orchidaceous plants, Dahlias, &c. These must not be confounded either with tubers or bulbs, as they have been by some writers, but are rather to be considered a special form of the root, to which the name of *Tubercules* (*fig.* 46.) would not be inapplicable. In Orchis the tubercules are often palmated

or lobed; in the Dahlia, and many Lilyworts, they hang in clusters, or are *fasciculated.*

fig. 46.

In internal structure the root differs little from the stem, except in being much more fleshy or woody; its cellular system, more especially, is subject to an unusually high degree of development in such plants as the Parsnip, and other edible roots. In Exogens, the mutual arrangement of the cellular and vascular systems of the root and stem is of absolutely the same nature. In many Endogens the roots are extremely perishable, usually annual, and their woody bundles form an imperfect hollow, or solid, cylinder, below the surface.

In Water lilies roots are deciduous, and have a definite position upon the rhizome, protruding from a cavity below the surface, resembling an air-hole. Of this curious fact the following account has been given by Munter :—

The entire surface of the rhizome of Nuphar lutea, the Yellow Water Lily, is coated with leaf-scars directed obliquely from above downwards, as in the stems of Cycads, and traces of the torn bundles of woody fibre are left on these scars. We do not, however, usually find any buds in the axils of the leaf-scars. A little below the scars of the leaves, we find single or grouped holes of the size of a pea, of a more or less rounded form, which are either arranged beneath the leaf-scars, or are only visible on those parts of the rhizome which are turned towards the soil. When these holes are grouped, three, five or six together, the lower ones are usually larger than the upper, and on minutely examining them we find a remarkable resemblance between each hole, and the cavity of the human acetabulum. In the former a circular

protuberance (limbus) surrounds the hole, as in the latter, but this has in addition a notch at its lower part; we then find on the inner surface of the pit a ring running parallel with the limb, *i. e.*, concentric; at the bottom of the pit a bundle of woody fibres, broken off, but still somewhat projecting, like the ligamentum teres of the human acetabulum. The surface of the pit between this woody bundle and the ring-shaped scar is smooth, and presents nothing remarkable. As regards the nature of these elegant pit-like scars, by comparing all parts of the surface, we soon perceive that they owe their origin to roots, which separate spontaneously; this view is confirmed by tracing the course of the separation. Even whilst the root is perfectly entire, the bark of the stem is raised from the surface of the latter, and gives rise to the above-mentioned limb. The concentric ring on the inner surface of the pit is formed by the separation of the bark of the root from that of the stem, and the broken-off woody bundle found in the bottom of the pit was previously continuous with the central woody bundle of the root. (*Annals of Natural History,* vol. xvi. p. 236.)

For a minute account of the Root the reader is referred to a paper by M. Auguste Trécul, in the *Annales des Sciences,* 3 series, vol. v. p. 340.

SECT. IV.—*Of the Appendages of the Axis.*

From the outside of the stem, but connected immediately with its vascular system, arises a variety of thin flat expansions, arranged with great symmetry, and usually falling off after having existed for a few months. These are called, collectively, appendages of the axis; and, individually, scales, leaves, bracts, flowers, sexes, and fruit. They must not be confounded with mere expansions of the epidermis, such as ramenta, already described (p. 158), from which they are known by having a connexion with the vascular system of the axis. Formerly botanists were accustomed to consider all these as essentially distinct organs; but, since the appearance of an admirable treatise by Goëthe in 1790, *On the Metamorphoses of Plants,* proofs of their being merely modi-

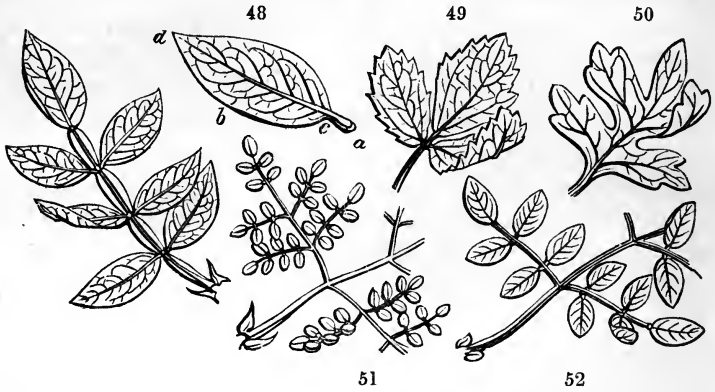
fications of one common type, the leaf, have been gradually discovered; so that that which, forty years ago, was considered as the romance of a poet, is now universally acknowledged to be an indisputable truth. It may, however, be remarked, that when those who first seized upon the important but neglected facts out of which this theory has been constructed, asserted that all appendages of the axis of a plant are metamorphosed leaves, more was stated than the evidence at that time would justify; for we cannot say that an organ is a metamorphosed leaf, when, in point of fact, it has never been a leaf. What was meant, and that which is supported by the most conclusive evidence, is, that every appendage of the axis is originally constructed of the same elements, arranged upon a common plan, and varying in their manner of development, not on account of any original difference in structure, but on account of special, local, and predisposing causes: of this plan the leaf is taken as the type, because it is the organ which is most usually the result of the development of those elements,—is that to which the other organs generally revert, when, from any accidental disturbing cause, they do not sustain the appearance to which they were originally predisposed,—and moreover, is that in which we have the most complete type of organisation.

Proof of this will be furnished as the different modifications of the appendages of the axis come respectively under consideration. The leaf, as the first that is formed, the most perfect of them all, and that which is most constantly present, is properly considered the type from which all the others are deviations, and is the part with the structure of which it is first necessary to become acquainted.

1. Of the Leaf.

The leaf is an expansion of the bark at the base of a leaf-bud, prior to which it is developed. In most plants it consists of cellular tissue, filling up the interstices of a network of fibres which proceed from within the stem, and ultimately separating from the bark by an articulation; in

many Monocotyledonous plants, Ferns and Mosses, no articulation exists, and the base of the leaf only separates from its parent stem by rotting away.



This difference of organisation has given rise to a distinction, on the part of Oken, between the articulated leaves of Dicotyledons and the inarticulated leaves of Monocotyledons and Acotyledons: the former he calls true leaves, and distinguishes by the name of *Laub;* the latter he considers foliaceous dilatations of the stem, analogous to leaves, and calls *Blatt.*

A leaf consists of two parts; namely, its stalk, which is called the *petiole* (*fig.* 48. *a*), and its expanded surface, which is called the *blade* or *lamina* (*fig.* 48. *c, b, d*): in ordinary language the latter term is not employed, but in very precise descriptions it is indispensable.

The point where the base of the upper side of a leaf joins the stem is called the *axil;* anything which arises out of that point is said to be *axillary.* If a branch or other process proceeds from above the axil, it is called *supra-axillary;* if from below it, *infra-axillary.*

The scar formed by the separation of a leaf from its stem is sometimes called the *cicatricule.* The withered remains of leaves, which, not being articulated with the stem, cannot fall off, but decay upon it, have been called *reliquiæ* or *induviæ,* and the part so covered is said to be *induviate.*

When leaves are placed in pairs on opposite sides of a stem (*fig.* 53.), and on the same plane, they are called *opposite:* if more than two are opposite, they then form what is called a

fig. 53.

whorl, or *verticillus:* but if they arise at regular distances from each other round the stem, and not from the same plane, they are then called *alternate.*

In plants having Exogenous stems, the first leaves,—namely, those which are present in the embryo itself (*cotyledons*),—are uniformly opposite; but those subsequently developed are either opposite, verticillate, or alternate in different species: on the contrary, in Endogens, the embryo leaf is either solitary, or, if there are two, they are alternate; and those subsequently developed are usually alternate also, but few cases occurring in which they are opposite. Hence some have formed an opinion that the normal position of the leaves of Exogens is opposite, or verticillate; and that when the leaves are alternate, this arises from the extension of a node; while that of Endogens is alternate, the whorls being the result of the contraction of internodes.

But it seems more probable that the normal position of all leaves is alternate, and their position upon the stem an elongated spiral, as is in many cases exceedingly apparent; for instance, in the genus Pinus, in Pandanus, which is actually named Screw-pine, in consequence of the resemblance its shoots bear to a screw, and in the Pine-apple: the Apple, the

Pear, the Willow, the Oak, will also be found to indicate the same arrangement, which is only less manifest because of the distance between the leaves, and the irregularity of their direction. If, in the Apple-tree for instance, a line be drawn from the base of one leaf to the base of another, and the leaves be then broken off, it will be found that a perfectly spiral line will have been formed. Upon this supposition, opposite or whorled leaves are to be considered the result of a peculiar non-development of internodes, and the consequent confluence of as many nodes as there may be leaves in the whorl. Rhododendron ponticum will furnish the student with an illustration of this: on many of its branches some of the leaves are alternate and others opposite; and several intermediate states between these two will be perceivable. In many plants, the leaves of which are usually alternate, there is a manifest tendency to the approximation of the nodes, and consequently to an opposite arrangement of the leaves, as in Solanum nigrum, and many other Nightshades; while, on the other hand, leaves which are usually opposite, separate their nodes and become alternate, as in Erica mediterranea: but this is more rare.

The best argument in support of the hypothesis that all whorls arise from the non-development of internodes and confluence of nodes, is, however, to be derived from flowers, which are several series of whorls, as will be seen hereafter. In plants with alternate leaves, the flowers often change into young branches, and then the whorls of which they consist are broken, the nodes separate, and those parts that were before opposite become alternate; and in monstrous Tulips, the whorls of which the flower consists are plainly seen to arise from the gradual approximation of leaves, which in their unchanged state are alternate.

A most elaborate memoir has been written by a German naturalist named Braun, to prove, mathematically, not only that the spiral arrangement is that which is everywhere visible in the disposition of the appendages of the axis, but that each species is subject to certain fixed laws, under which the nature of the spires, and in many cases their number,

are determined. The original appeared in the *Nova Acta of the Imperial Academy Naturæ Curiosorum;* and a very full abstract of it has been given by Martins, in the first volume of the *Archives de Botanique,* from which I borrow what follows:—

"The scales of the fruit of Coniferous plants are nothing but carpellary leaves, which do not form, like the floral envelopes of other plants, a complete cavity surrounding the sexual organs on all sides, but which are slightly concave, and protect them on one side only. This point admitted, if we consider attentively the cone of a Pine, or of a Spruce Fir, we are at once led to inquire whether the scales are arranged in spires or in whorls. Breaking through its middle a cone of Pinus Picea (Silver Fir), we remark three scales, which at first sight appear to be upon the same plane; but a more attentive examination shows that they really originate at different heights, and moreover, that they are not placed at equal distances from each other; so that we cannot consider them a whorl, but only a portion of a very close spiral. But, considering the external surface of the cone viewed as a whole, we find that the scales are disposed in oblique lines, which may be studied—1. As to their *composition,* or the number of scales requisite to form one complete turn of the spire; 2nd. As to their *inclination,* or the angle, more or less open, which they form with their axis; 3d. As to their total number, and their arrangement round the common axis, which constitutes their *co-ordination.* Finally, we may endeavour to ascertain whether the spires turn from right to left, or *vice versâ.*

He then proceeds to show, that the spiral arrangement is not only universal, but subject to laws of a very precise nature. The evidence upon which this is founded is long and ingenious, but would be unintelligible without the plates which illustrate it. I must, therefore, content myself with mentioning the results. Setting out from the Pine cone above referred to, he found that several series of spires are discoverable in the arrangement of their scales, and that there invariably exists between these spires certain arith-

metical relations, which are the expression of the various combinations of a certain number of elements, disposed in a regular manner. All the spires depend upon the position of a fundamental series, from which the others are deviations. The nature of the fundamental series is expressed by a fraction, of which the numerator indicates the whole number of turns required to complete one spire, and the denominator the number of scales or parts that constitute it. Thus $\frac{8}{21}$ indicates that eight turns are made round the axis before any scale or part is exactly vertical to that which was first formed, and the number of scales or parts that intervene before this coincidence takes place is 21.

The following are some of the results thus obtained by Braun, in studying the composition of the spires of different plants:—

$\frac{1}{2}$ in Asarum, Aristolochia, Lime tree, Vetch, Pea, the spikes of all grasses.

$\frac{1}{3}$ is rare in Dicotyledons, and generally changes into more complicated spires. It exists in Cactus speciosus, and some others.

$\frac{2}{5}$ is the most common of all, and represents the quincunx. Mezereum, Lapsana communis, Polemonium cœruleum, Potato, are examples.

$\frac{3}{8}$ is also common, as in the Bay-tree, the Holly, common Aconite, and the tuft of radical leaves of Plantago media.

$\frac{5}{13}$ exists where the leaves are numerous and their intervals small. Wormwood, common Arbutus, dwarf Convolvulus, and the tufts of leaves in London Pride and Dandelion, are instances.

$\frac{8}{21}$ in Woad, Plantago lanceolata, the bracts of Digitalis lanata.

$\frac{13}{34}$ in Sempervivum arboreum, the bracts of Plantago media, and of Protea argentea.

$\frac{21}{55}$ was found on an old trunk of Zamia horrida, and two species of Cactus (coronarius and difformis).

It does not, however, appear that this inquiry has led to any thing beyond the establishment of the fact, that, beginning from the cotyledons, the whole of the appendages

of the axis of plants—leaves, calyx, corolla, stamens, and carpels—form an uninterrupted spire, governed by laws which are nearly constant. No application of the doctrine appears practicable, except to assist in the distinction of species, for which it would be well adapted, if the determination of the series with the requisite precision were less difficult; this is shown in the following instances of differences in the fundamental spire in nearly allied species.

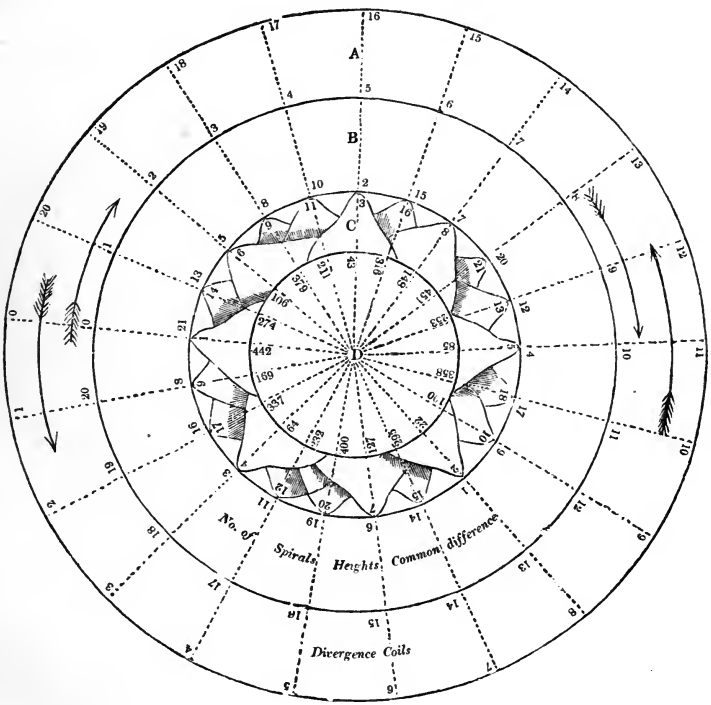
Pinus pinaster, $\frac{2}{5}\frac{1}{5}$—sylvestris, $\frac{1}{3}\frac{3}{4}$—cembra, $\frac{8}{2}\frac{}{1}$—larix, $\frac{8}{2}\frac{}{1}$—microcarpa, $\frac{2}{5}$.

Betula alba and pubescens, $\frac{8}{2}\frac{}{1}$ and $\frac{1}{3}\frac{3}{4}$—fruticosa generally, $\frac{5}{1}\frac{}{3}$.

Corylus avellana, $\frac{8}{2}\frac{}{1}$—americana and tubulosa, $\frac{1}{3}\frac{3}{4}$ in their male catkins.

The whole of this curious question has been simplified by

fig. 54.



Professor Henslow, in observations printed for private circulation; and I am happy to be able, by the permission of their author, to lay them in this place before the public.

"The scales on a cone of the Spruce Fir (*Abies excelsa*) are placed spirally round the axis, at equal intervals; and after eight coils of the spiral, the twenty-second scale ranges vertically over the first. If this arrangement be referred to a cylinder, and then projected on a plane cutting its axis at right angles, the angular distance (*Divergence*) between two contiguous scales, seen from the centre, is $\frac{1}{21}$ of the circumference. Hence the divergence of the generating or primary spiral $\frac{8}{21}$. The various peculiarities of the secondary spirals which result from the above arrangement, may be seen by inspecting *fig.* 54.

A. If any figure in this circle represent the divergence of a spiral, the same will also represent the number of coils which that spiral must make before the twenty-second scale upon it comes vertically over the first.

B. The figures in this circle (corresponding to the several divergencies in A.) show the number of similar and parallel spirals which must be coiled round the cylinder, in order that *every* scale may range upon them.

The same figures also indicate the height of each spiral—viz.: either the *comparative* lengths of the vertical lines between scales 1. and 22. or the distance between two horizontal circles through scales 1. and 2.; and, lastly,

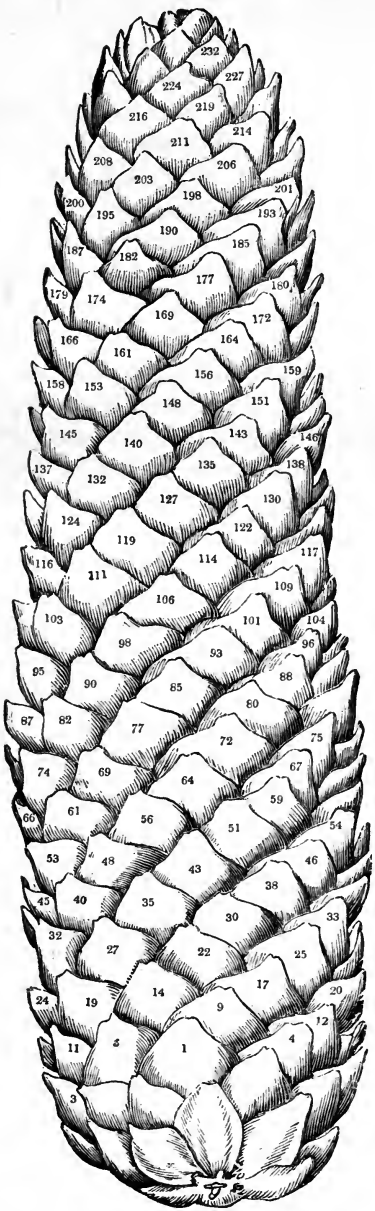
These figures are the *common differences* in the different arithmetic series apparent on the consecutive scales of each spiral.

C is the arrangement of the first twenty-one scales on the generating spiral.

D shows the number on the scales which begin a *second series* of each kind of spiral, *i. e.* the numbers on their twenty-second scales.

N.B. The number on the scale which begins a fresh series of *any* spiral is found by the formula (a + 21 B) where (a) = the number on the scale beginning a former series of the spiral, and B the common difference of the numbers on two contiguous scales.

fig. 55.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Ex. Gr. Considering the spiral (*fig.* 55.) through the scales 1. 9. 17. &c., 153. 161. 169. &c. A. 1st, Its divergence (from 1 to 9) is 100—20, and, 2nd, It must coil once towards the left, or twenty times towards the right (of a spectator at the axis) before it passes through the twenty-second scale upon it (viz. No. 169.), which ranges vertically over the first. B. 1st, There are seven other similar spirals parallel to it. 2nd, Their height (as from 1 to 169) = eight times the height from 1 to 22; and, 3rd, The common difference of the numbers of the scales is also eight. The position of the several *beginnings* of the 8 spirals (viz. on Nos. 1. to 8.) is shown in C; and in D we have the numbers (169. 106. 43. &c.) which respectively begin the second series of each spiral.

To discover the primary spiral, we may fix on any scale as a point of departure (No. 1.), and then, by numbering the scales on two of the secondary spirals (as 1. 9. 17. &c., and 1. 6. 11. &c.) which proceed in opposite directions, we may afterwards very readily place the numbers on all the scales. The easiest method of obtaining the common differences (viz. 8 and 5), for the purpose of numbering the scales in the two cases selected, is to draw a circle round the cone, and count the number of each of the two kinds of spirals intersecting it (which will be 8 of the first and 5 of the second). When a secondary spiral perfects a complete coil (as 1. 9. &c. 161. 169.), the number of the spirals of the same kind is readily seen; but the former mode for obtaining this number will apply equally well to cases where the cone is too short for the coils to be completed."

Professor Link has the following additional observations on this subject:—"Since Schimper much has been written upon the position of the leaves and bracts on the stem, although few mathematical researches have appeared upon the subject, which is, nevertheless, well adapted to such inquiries. A natural philosopher of considerable merit in the department of mathematical crystallography, Herr Naumann, has published an essay 'On the Quincunx, as the fundamental basis of the arrangement of Leaves,' (Ueber den Quincunx als Grundgesetz der Blattstellung im Pflanzenreiche; in Poggendorf's *Annal. d. Physik. u. Chemie,* 2 Reihe,

b. 26, 1842, s. l.) The author first adverts to the regular arrangement of the scars in such fossil plants, as Lepidodendron and Sigillaria; premising, however, that he has no pretension to be a botanist, and is chiefly acquainted with what Carl Schimper and Alex. Braun have previously done in this matter. Although it is true that nature does not work in organic bodies by square and compass, still it is probable that her forms have always some geometrical basis.

"A quincunxial arrangement," says the author, "is always found where parallel series or rows (or also series radiating from a common point, and inclined at the same angle) of equidistant points are formed in such a manner, that the points of each individual series do not correspond with those of the neighbouring series, but are opposed to a defined part of the space intervening between two points. If we make the distance between the points of each series = a, the distance or interval of the individual parallel series = b, and if $\frac{n}{m}$ be a fraction whose numerator may at the farthest be half as great as the denominator, then the quincunx will be constituted from this, that all the points of the second series are removed from a direct parallelism with those of the first series by $\frac{n}{m}$ a.

The first point considered is the quincunx of parallel series. The whole arrangement in this case will have completed a cycle in m series; and hence the numerator of the fraction $\frac{n}{m}$ is to be regarded as the proper cyclical number of the quincunx. To determine the oblique lines which Schimper called spirals (wendel), and which our author terms *strophes*, he draws two right-angled coordinates through a figure, which represents the superficies of a cylinder, with the quincunx projected on a plane. One side of the ordinates may be called the positive, the other the negative. If now we join any point in the line of the ordinates with the nearest point of the neighbouring series, $\frac{n}{m}$ a, we obtain a line, by the production of which a complete series of points is constituted, and we have also a complete system of similar series parallel to each other. These series are the first and most important strophes. The author calls them *Archistrophes*,

and distinguishes them as first, second, and third archistrophe, &c. If we now draw straight lines from the points of origin of the coordinates to all the points of the Archistrophes, we get the secondary strophes, and the author calls the strophes described through the points of the second archistrophe, *protostrophes,* as also those through the points of the third archistrophe, *deuterostrophes,* &c. They are also designated, according to the number of the point in each archistrophe, strophes of the first, second, third order, and so forth. The ordinal number of each archistrophe towards which any secondary strophe runs, when diminished by 1, thus determines the class, and the ordinal number the point in such archistrophe points out the order of the strophe. The author calls this the distinguishing point of the strophe, and if its coordinates x and y are represented in general by α and β, it readily follows that the pth point of the $(q-1)$ th archistrophe will be determined by the coordinates $\alpha=\frac{m-qn}{m}a$, and $\beta=pb$. These two equations form the groundwork of the investigation of quincunxes of parallel series. In the second division Mr. Naumann treats of the circular or concentric quincunx, where, namely, the leaves or similar parts stand on a spherical disc, which, however, occurs but seldom in the vegetable kingdom."

"I have," adds Link "(in my *Grundlehre der Kraüterkunde,* 2nd edit., part i., pp. 446, 447 et seq.), given a mathematical statement of the matter, which seems to me very simple, and which rests on the fact that leaves or bracts are drawn out into a spiral line from their circular position. To determine this change of position, I have taken the angle at which the secondary series are inclined to a directly ascending primary series. Thus, from the angular distances of the whorls or strophes from the principal line, we may determine the number of revolutions which are made by the leaves or bracts, between any given leaf or bract, and that which is situated in a straight line above it. This calculation has here, principally, only a general application to different cases; the enumeration and measurement must be made upon the plant itself, since organic digressions from the fundamental form do not admit of accurate measurement." (*Ray Reports,* 1845, p. 347).

It is obvious that the hypothesis of the spiral arrangement of the foliaceous organs of plants is a mathematical question having but little relation to Botany. Those who wish to investigate it, will find much more concerning it in *Steinheil's* Observations upon the Theory of Phyllotaxis, in *Ann. Sc.* n. s. IV. 100. 142, *Bravais,* sur la disposition des feuilles curvisériées, ib. VII. 42. and VIII. 161., *Link,* Elementa Botanica, ed. 2. II. 448., *Dutrochet,* Mémoires, I. 238.

In their normal state the edges of leaves are distinct, both from each other and from the stem. But, in some cases, adhesions of various kinds occur, and give them a new character. Thus, in Cardui, and many other thistle-like plants, the elongated bases of the leaves adhere to the stem, and become what is called *decurrent.* The elevated lines upon the stem, thus formed, are called by Link and Klotzsch *sterigmata : vera,* when traversed by a cord of vessels ; *spuria,* when mere elevated cellular plates. In Bupleurum perfoliatum the lobes of the base of the leaf not only cohere with the stem, but projecting beyond it, grow together, so as to resemble a leaf through which the stem has pierced : this is called being *perfoliate.* Frequently two opposite leaves grow together at the base, as in Caprifolium perfoliatum ; to this modification the latter term is often also applied, but that of *connate* is what more properly belongs to it.

The usual anatomical structure of the leaf is this :—From the medullary sheath, or in Endogens, the woody bundles, diverges a bundle of woody tissue, accompanied by spiral vessels : this passes through the bark, and proceeds, at an angle more or less acute, to a determinate distance from the stem, branching off at intervals, and, by numerous ramifications, forming a kind of network. At the point of the stem whence the bundle of fibro-vascular tissue issues, the cellular tissue of the bark, mesophyll or cortical integument, also diverges, accompanying the fibro-vascular tissue, expanding with its ramifications, and filling up their interstices. The tissue that proceeds from the medullary sheath, after having passed from the origin of the leaf to its extremity,

doubles back upon itself, forming underneath the first a new layer of fibre, which, upon its return, converges just as the first layer diverged, at length combining into a single bundle, corresponding in bulk and position to that which first emerged, and finally discharging itself into the liber. If, therefore, a section of the leaf and stem be carefully made at a node, it will be found that the bundle of woody tissue which forms the frame-work of the leaf communicates above with the medullary sheath, and below with the liber. This is easily seen in the spring, when the leaves are young; but is not so visible in the autumn, when their existence is drawing to a close. The double layer of fibro-vascular tissue is also perceptible in a leaf which has lain during the winter in some damp ditch, where its cellular substance has decayed, so that the cohesion between the upper and lower layers is destroyed, and the latter can be easily separated. The curious leaves of Hermas which have the property of opening, upon slight violence, like the leg of a silk stocking, so that the hand may be thrust between their upper and lower surfaces, derive that singular separability from an imperfect union between the layer of excurrent and recurrent fibre. The veins do not, however, always consist of a double layer of fibro-vascular tissue. An instance to the contrary is mentioned by me in the *Elements of Botany*, as being "furnished by Theophrasta Jussiæi. In this plant three layers of veins occur of which the middle is much reticulated, but the upper and lower are far less so, their fibres lying much more parallel with each other, and instead of being applied to the reticulations of the middle layer covering it obliquely." In reality the anatomy of the veins of leaves has been little studied, and must be regarded as a branch of vegetable anatomy, at present not at all well understood.

De Candolle remarks, that, when the fibres expand to form the limb of a leaf, they may (whether this phenomenon occurs at the extremity of a petiole, or at the point of separation from the stem) do so after two different systems: they may either constantly preserve the same plane, when common flat leaves are formed; or they may expand in any direction, when cylindrical or swollen or triangular leaves are the

result. (*Organogr.* p. 270.) Cylindrical leaves are, however, sometimes produced otherwise, as is proved by Brasavola venosa, whose leaf is just intermediate between the flat fleshy leaf of Br. glauca and the absolutely terete species. This shews that in the latter the leaf owes its peculiar appearance in part to a general thickening of its parenchym, and in part to the edges turning inwards, meeting and growing together. And this is probably also the origin of the terete leaves found in other Orchids, such as species of Vanda, Luisia, and Dendrobium, as is indicated by the channel which usually runs along their upper side.

The cellular tissue of which the rest of the leaf is composed is parenchym, which Link then calls *diachyma,* or that immediately beneath the two surfaces *cortex,* and the intermediate substance *diploe.* De Candolle calls these two, taken together, the *mesophyllum.* The whole is protected, in leaves exposed to air, by a homogeneous cuticle of indurated organic mucus (p. 1.), and a coating of epidermis, furnished with stomates; but in submersed leaves the parenchym is naked, no epidermis overlying it.

The general nature of the parenchymatous part of leaves has been explained, both by Link and others, and figured by Mohl, firstly in 1828 (*Uber die Poren des Pflanzenzellgewebes,* tab. i. fig. 4, &c.), and afterwards in his elaborate inquiry into the anatomy of Palms. A very complete account is that of Adolphe Brongniart, in 1830 (*Annales des Sc.* vol. xxi. p. 420.), of which much of what follows is an abstract.

The epidermis is a layer of vesicles adhering firmly to each other, and sometimes but slightly to the subjacent tissue, from which they are entirely different in form and nature: in form, for their cellules are depressed, and, in consequence of the variety of outline that they present, arranged in meshes either regular or irregular; and in nature, because these bladders are perfectly transparent, colourless, and probably filled with either air or rarefied fluid,—for the manner in which light passes through them proves that they do not contain dense fluid. They scarcely ever contain any organic particles, and are probably but little permeable either to fluids or gaseous matters; while, on the other hand, the

vesicles of the subjacent parenchym are filled with the green substance which determines the colour of the leaf. The epidermis is not always formed of a single layer of vesicles, but in some cases consists of two, or even three. No trace is discoverable of vessels either terminating in or beneath the cuticle; Brongniart states this most explicitly, and my own observations are in accordance with his: an opinion, therefore, which some botanists have entertained, that spiral vessels terminate in the stomates (D. C. *Organogr.* p. 272. &c.), must be abandoned. At the margin of a leaf the epidermis is generally harder than elsewhere, and sometimes becomes so indurated as to assume a flinty texture, as in the Sedges, and many other plants.

Stomates are found upon various parts of the epidermis: in some plants only on that of the under side of leaves, in others on the upper also; in floating leaves upon the latter only. When leaves are so turned that their margins are directed towards the earth and the heavens, the two faces are then alike in appearance, and are both equally furnished with stomates. In succulent leaves they are said to be either altogether absent or very rare; but this is not exactly the fact. They are fewer and smaller, and perhaps more imperfect, in succulent than in other parts, but by no means absent. According to the observations of De Candolle (*Organogr.*, p. 272.), they are, in the Orange and Mesembryanthemum, as ten in the former to one in the latter.

I have remarked (*Bot. Reg.* 1540.) the singular fact, that certain plants have the power of forming stomates on the upper surface of their leaves, if from any cause their leaves are inverted. Thus the stomates are usually upon the under side of leaves, where also the veins are more prominent, and hairs appear exclusively, if hairs are found upon only one of the two surfaces. In Alströmeria that side of the leaves which is organically the undermost becomes, in consequence of a twist in the petiole, the uppermost, and that side which is born uppermost is turned undermost; and then the organic underside, being turned uppermost, has no stomates; while the organic upper side, being turned downwards, although under other circumstances it would have neither stomates,

hairs, nor elevated veins, acquires all those characters in consequence of its inversion.

A very curious observation, in connection with this subject, has been made by Mirbel, in his memoir upon the structure of Marchantia polymorpha. The young bulbs by which this plant is multiplied are originally so homogeneous in structure, that there is no apparent character in their organisation to show which of their faces is destined to become the upper surface, and which the under. For the purpose of ascertaining whether there existed any natural but invisible predisposition in the two faces to undergo the changes which subsequently become so apparent, and by means of which their respective functions are performed, or whether the tendency is given by some cause posterior to their first creation, the following experiments were instituted :—Five bulbs were sown upon powdered sandstone, and it was found that the face which touched the sandstone produced roots, and the opposite face formed stomates. It was, however, possible that the five bulbs might have all accidentally fallen upon the face which was predisposed to emit roots; other experiments of the same kind were therefore tried, first with eighty, and afterwards with hundreds of little bulbs,—and the result was the same as with the five. This proved that either face was originally adapted for producing either roots or stomates, and that the tendency was determined merely by the position in which the surfaces were placed. The next point to ascertain was, whether the tendency once given could be afterwards altered. Some little bulbs, that had been growing for twenty-four hours only, had emitted roots; they were turned, so that the upper surface touched the soil, and the under was exposed to light. In twenty-four hours more the two faces had both produced roots: that which had originally been the under surface went on pushing out new roots; that which had originally been the upper surface had also produced roots: but in a few days the sides of the young plants began to rise from the soil, became erect, turned over, and finally recovered in this way their original position, and the face which had originally been the uppermost immediately became covered with stomates. It, therefore, appears that, the impulse once given,

the predisposition to assume particular appearances or functions is absolutely fixed, and will not change in the ordinary course of nature. This is a fact of high interest for those who are occupied with researches into the causes of what is called vegetable metamorphosis.

The parenchym is, if casually examined, or even if viewed in slices of too great thickness, apparently composed of heaps of small green bladders, arranged with little order or regularity; but if very thin slices are taken and viewed with a high magnifying power, it will be seen that nothing can be more perfect than the plan upon which the whole structure is contrived, and that, instead of disorder, the most wise order pervades the whole. Upon this subject I extract the words of Adolphe Brongniart:—

"There exists beneath the upper cuticle two or three layers of oblong blunt vesicles, placed perpendicular to the surface of the leaf, and generally much less in diameter than the bladders of the cuticle; so that they are easily seen through it. These vesicles, which appear specially destined to give solidity to the parenchym of the leaf, have no other intervals than the little spaces that result from the contact of this sort of cylinder: nevertheless, in plants that have stomates on the upper surface of their leaves, as is the case in most herbaceous plants, and in such as float on the surface of water, there exist here and there among the vesicles some large spaces, through which the stomates communicate with the interior of the leaf. This parenchym is entirely different from what is found beneath the cuticle of the lower side. There, instead of consisting of regular cylindrical vesicles, it is composed of irregular ones, often having two or three branches, which unite with the limbs of the vesicles next them, and so form a reticulated parenchyma; the spaces between whose vesicles are much larger than the vesicles themselves. It is this reticulated tissue, with large spaces in it (to which the name of cavernous or spongy parenchyma might not improperly be applied), that, in most cases, occupies at least half the thickness of the leaves between the veins. The arrangement of the vesicles is very obvious if the lower cuticle of certain leaves be lifted up with the layer of

parenchyma that is applied against it; it may then be seen that these anastomosing vesicles form a net with large meshes —a sort of grating—inside the cuticle. It must not, however, be supposed that this structure, which I have remarked in several Ferns, and in a great many dicotyledonous plants, is without exception. In many monocotyledonous and succulent plants we have some remarkable modifications of this structure. Thus, in the Lily, and several plants of the same family, the vesicles of parenchyma that are in contact with the lower cuticle are lengthened out, sinuous, and toothed, as it were, at the sides: these projections join those of the contiguous vesicle; and a number of cavities is the consequence, which render this sort of parenchyma permeable to air. An analogous arrangement exists in the lower parenchyma of Galega. In the Iris, there is scarcely any space between the oblong and polyhedral vesicles which form the parenchyma; but it is remarked, that the subjacent parenchyma is wanting at every point where the cuticle is pierced by a stomate. In such succulent plants as I have examined, the spaces between the cellules of parenchyma are very small; but, nevertheless, here and there, there are often larger cavities, which either correspond directly with the stomates, or are in communication with them. The same thing happens in plants with floating leaves, where the stomates placed on the upper surface correspond with the layer of the cylindrical and parallel vesicles; in such case there are, here and there, between these vesicles, empty spaces which almost always correspond to the points where the stomates exist, and which permit the air to penetrate between the vesicles as far as the middle of the parenchyma of the leaf."

Thus much Adolphe Brongniart; who adds, that in submersed leaves there is no cuticle, but the whole consists of solid parenchym alone, in which there are no other cavities than such as are necessary to float the leaves. The observations of Mohl, Meyen, and myself generally confirm this; but, at the same time, numerous cases exist in which the texture of the leaf has been found to be nearly the same throughout; in fact, the only circumstance which is found to be uniform in respect to the internal anatomy of leaves is,

that their parenchyma is cavernous, and that the air cavities are uniformly in communication with the stomates.

Dutrochet states in addition (*Ann. des Sc.*, xxv. 245.), that the interior of a leaf is divided completely by a number of partitions covered by the ribs and principal veins, so that the air cavities have not actually a free communication in every direction through the parenchym; but are, to a certain extent, cut off from each other. This is conformable to what Mirbel has described in Marchantia, where the leafy expansions are separated by partitions into chambers, between which, he is of opinion, there is no other communication than what results from the permeability of the tissue.

The veins being elongations of the medullary sheath, necessarily consist of woody tissue and vessels, to which is added cinenchymatous tissue. In submersed leaves spiral vessels are often wanting, the veins consisting of nothing but woody tissue.

Such are the general anatomical characters of leaves; but it must be borne in mind, that, in different species, they undergo a variety of remarkable modifications. These arise either from the addition of parenchym, when leaves become *succulent*, or from the non-development of it when they become *membranous*, or from the total suppression of it, and even of the veins also in great part, as in those which are called *ramentaceous*, such as the primordial leaves of the genus Pinus. Occasionally, the veins only are formed, the parenchym being deficient, as in Ranunculus aquatilis, the very curious Hydrogeton or Ouvirandra, and various species of Podostemads.

It has already been seen that a leaf may consist of two distinct parts; the *petiole*, or stalk, and the *lamina*, or blade; both of these demand separate consideration. These are, however, not necessarily present; the petiole may exist without the lamina, as in *leafless* Acacias, or the lamina without the petiole, in all *sessile* leaves.

The BLADE, *lamina* (or *limbus*, as it is called by some) is subject to many diversities of figure and division; most commonly it forms an approach to oval, being longer than broad.

It is described by two opposite arcs, whose points of intersection are the apex and base.

That extremity of the blade which is next the stem is called its *base;* the opposite extremity, its *apex;* and the line representing its two edges, the *margin* or *circumscription.*

If the blade consists of one piece only, the leaf is said to be *simple,* whatever may be the depth of its divisions: thus, the entire blade of the Box tree, the serrated blade of the Apple leaf, the toothed blade of Coltsfoot, the runcinate blade of Taraxacum, the pinnatifid blade of Hawthorn (which is often divided almost to its very midrib), are all considered to belong to the class of simple leaves. But if the petiole branches out, separating the cellular tissue into more than one distinct portion, each forming a perfect blade by itself, such a leaf is often said to be *compound,* whether the divisions be two, as in the conjugate leaf of Zygophyllum, or indefinite in number, as in the many varieties of pinnated leaves. Another notion of a compound leaf consists in its divisions being articulated with the petiole, by which it is better distinguished from the simple leaf than by the number of its divisions. Thus, the pedate leaf of a Hellebore or an Arum, both in this sense belong to the class of simple leaves; while the solitary blade of the Orange, the common Barberry, &c. are referable to the class of compound leaves. This distinction has been thought to be of some importance to the student of natural affinities; for, while division of whatever degree may be expected to occur in different species of the same genus or order (provided there is no articulation), it rarely happens that such compound leaves, as are articulated with their petiole, are found in the same natural assemblage with those in which no articulation exists. Alphonse De Candolle remarks, however, that in Gleditschia, whose leaves are mostly articulated, we find some leaves with their leaflets united, and therefore not articulated with their midrib; and this, and other similar instances, diminishes the value of articulation as the test of a compound leaf; moreover, in such apparently simple leaves as those of Zamia, the leaflets are, in fact, articulated with their midrib, as is proved by macerating them, when they spontaneously disarticulate.

In speaking of the *surface* of a leaf it is customary to make use of the word *pagina*. Thus, the upper surface is called *pagina superior;* the lower surface, *pagina inferior*. The upper surface is more shining and compact than the under, and less generally clothed with hairs; its veins are sunken; while those of the lower surface are usually prominent. The epidermis readily separates from the lower surface, but with difficulty from the upper. There are frequently hairs upon the under surface while the upper is perfectly smooth; but there are few instances of the upper surface being hairy while the lower is smooth.

The ramifications of the petiole among the cellular tissue of the leaf are called *veins*, and the manner of their distribution is termed *venation*. This influences in a great degree the figure and general appearance of the foliage.* The vein which forms a continuation of the petiole and the axis of the leaf is called the midrib or *costa:* from this all the rest diverge, either from its sides or base. If other veins similar to the midrib pass from the base to the apex of a leaf, such veins have been named *nerves;* and a leaf with such an arrangement of its veins has been called a *nerved* leaf. In speaking of these parts, a leaf is said to be *three,* or *five,* or otherwise *nerved,* if the so-called nerves all proceed from the very base of the lamina, but it is called *triple, quintuple,* &c. *nerved,* if the nerves all proceed from above the base of the lamina. If the veins diverge from the midrib towards the margin, ramifying as they proceed, such a leaf has been called a *venous* or *reticulated* leaf. This is the sense in which these terms were used by Linnæus; but Link and some others depart from so strict an application of them, calling all the veins of a plant nerves, whatever may be their origin or direction.

The veins are, however, improperly called nerves, either in all cases, as by Link, or in certain cases only, when they have

* Dr. Dickie is, however, of a different opinion, and thinks "that it cannot be said that the forms of leaves in flowering plants have any dependence whatever on their venation, since young leaves are lobed, &c., previous to the appearance of the veins. The truth he believes to be, that the quantity of cellular tissue in a leaf determines the development and position of the veins, and not the reverse." (*Annals of Natural History,* xi. 322.)

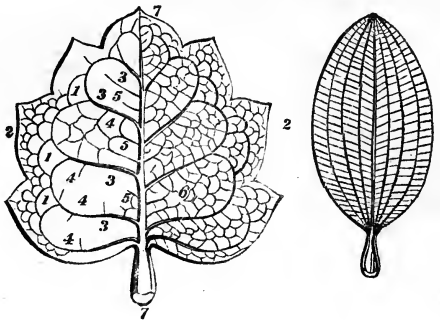
a particular size or direction, as by Linnæus and his followers. Nothing is more destructive of accurate ideas in natural history than giving names well understood in one kingdom of nature to organs in another kingdom of a different kind, unless it is the, perhaps, more reprehensible practice of giving two names conveying different ideas to the same organ in the same kingdom of nature. Thus, when the veins of a plant are termed nerves, it is naturally understood that they exercise functions of a similar nature to those of the nerves of animals: if otherwise, why are they so called? But they exercise no such functions, being mere channels for the transmission of fluid. Again, if one portion of the skeleton of a leaf is called a vein, and another portion a nerve, this apparently precise mode of speaking leads yet more strongly to the belief that the structure and function of those two parts are as widely different as the structure and function of a vein and a nerve in the animal economy; else why should such caution be taken to distinguish them? But, in fact, there is no difference whatever, except in size, between the veins and nerves of a leaf. In order to obviate the inconvenience of using the word nerve, the term *nervure* is now often substituted.

For the sake of obtaining great precision in describing such a very important and various-formed organ as the leaf, many terms have been invented, especially by Link and De Candolle, which, although not used in daily parlance, are important where brevity and precision are required. Without exactly adopting the nomenclature of either of these distinguished writers, it appears that upon it a system of names may be founded, to which the systematist can have little to object.

It has been usual to call that bundle of vessels only which passes directly from the base to the apex of a leaf the *rib*, or *costa*, or midrib. This term should be extended to all main veins proceeding directly from the base to the apex, or to the points of the lobes. There is no difference in size in these ribs; and in lobed leaves, which may be understood as simple leaves approaching composition, each rib has its own particular set of veins.

The midrib (*fig.* 56. 7) sends forth alternately, right and left along its whole length, ramifications of less dimensions

fig. 56.



than itself, but more nearly approaching it than any other veins: these may be called *primary veins* (*fig.* 56. 3). They diverge from the midrib at various angles, and pass to the margin of the leaf, curving towards the apex in their course, and finally, at some distance within the margin, forming an anastomosis with the back of the primary vein, which lies next them. That part of the primary vein which is between the anastomosis thus described, having a curved direction, may be called the *curved vein.* Between this latter and the margin, other veins, proceeding from the curved veins, with the same curved direction, and of the same magnitude, occasionally intervene: they may be distinguished by the name of *external veins* (*fig.* 56. 1). The margin itself and these last are connected by a fine net-work of minute veins, which I would distinguish by the name of *marginal veinlets.* From the midrib are generally produced, at right angles with it, and alternate with the primary veins, smaller veins; which may not improperly be named *costal veins* (*fig.* 56. 5). The primary veins are themselves connected by fine veins, which anastomose in the area between them; these veins, when they immediately leave the primary veins, I would call *proper veinlets* (*venulæ propriæ*) (*fig.* 56. 4); and where they anastomose, *common veinlets* (*ven. communes*). The area of parenchyma, lying between two or more veins or veinlets, I name with the old botanists *intervenium.*

These distinctions may to some appear over-refined; but I am convinced that no one can very precisely describe a leaf without the use either of them, or of equivalent terms yet to be invented. With respect to their venation only, leaves may be conveniently arranged under the following heads:—

1. *Veinless* (*avenium*), when no veins at all are formed, except a slight approach to a midrib, as in Mosses, Fuci, &c. Leaves of this description exist only in the lowest tribes of foliaceous plants, and must not be confounded with the fleshy or thickened leaves common among the higher orders of vegetation, in which the veins are by no means absent, but only concealed within the substance of the parenchyma. (See No. 10.) Of this De Candolle has two forms,—first, his *folia nullinervia,* in which there is not even a trace of a midrib, as in *Ulva;* and second, his *folia falsinervia,* in which a trace of a midrib is perceptible. These terms appear to me unnecessary; but, if they be employed, the termination *nervia* must be changed to *venia.*
2. *Equal-veined* (*æqualivenium*), when the midrib is perfectly formed, and the veins are all of equal size, as in Ferns. This kind of leaf has not been before distinguished: it may be considered intermediate between those without veins and those in which primary veins are first apparent. The veins are equal in power to the proper veinlets of leaves of a higher class.
3. *Straight-veined* (*rectivenium*). In this the veins are entirely primary, generally very much attenuated, and arising from towards the base of the midrib, with which they lie nearly parallel: they are connected by proper veinlets; but there are no common veinlets. The leaves of Grasses and of Palms and Orchidaceous plants are of this nature. This form has been called by Link *paralleli-* and *convergenti-nervosum,* according to the degree of parallelism of the primary veins; and to these two he has added what he calls *venuloso-nervosum,* when the primary veins are connected by proper veinlets; but as this is always so, although it is not in all cases equally apparent, the term is superfluous. Ach. Richard calls

this form *laterinervium,* and De Candolle *rectinervium;* from which I do not find it advisable to distinguish his *ruptinervium,* which indicates the straight-veined leaf, when the veins are thickened and indurated, as in the Palm tribe. Straight-veined leaves occur generally in Endogens, and, slightly modified, are one of the characteristic marks of Epacrids. Some Botanists regard leaves with this kind of venation as consisting of petiole only; but I am unacquainted with any fact which confirms this view.

4. *Curve-veined* (*curvivenium*). This is a particular modification of the last form, in which the primary veins are also parallel, simple, and connected by unbranched proper veinlets; do not pass from near the base to the apex of the leaf, but diverge from the midrib along its whole length, and lose themselves in the margin. This is the *folium hinoideum* and *venuloso-hinoideum* of Link, the *f. penninervium* of A. Richard, and the *f. curvinervium* of De Candolle. It is common in the whole Musal alliance, and is unknown except among Endogens. It is supposed by the last-named Botanist that this also ought to be regarded as a peculiar modification of petiole (a kind of phyllode), rather than as a true leaf analogous to those next to be described.
5. *Netted* (*reticulatum*). Here the whole of the veins which constitute a completely developed leaf are present, arranged as I have above described them, there being no peculiar combination of any class of veins. This is the common form of the leaves of Dicotyledons, as of the Lilac, the Rose, &c. It is the *folium venosum* of Linnæus, the *f. indirectè venosum* of Link, the *f. mixtinervium* of A. Richard, and the *f. retinervium* of De Candolle. If the external veins and marginal veinlets are conspicuous, Link calls this form *combinatè venosum;* but if they are indistinct, he calls it *evanescentè venosum.*
6. *Ribbed* (*costatum*). In this three or more midribs proceed from the base to the apex of the leaf, and are connected by branching primary veins of the form and magnitude of proper veinlets, as in Melastoma. This must not be

confounded with the *straight-veined* leaf, from which it may in all cases of doubt be distinguished by the ramified veins that connect the ribs. This is a very material difference, which has never been properly explained. Linnæus and his followers confound the two forms; but modern writers separate them: although it must be confessed that it is difficult to discover their distinctions from the characters hitherto assigned to them. Link calls these leaves *f. nervata,* A. Richard *f. basinervia,* and De Candolle *f. triplinervia* and *f. quintuplinervia.* If a ribbed leaf has three ribs springing from the base, it is said to be *three-ribbed* (*tri-costatum, trinerve* of authors); if five, *five-ribbed,* and so on. But if the ribs do not proceed exactly from the base, but from a little above it, the leaf is then said to be *triple-ribbed* (*tripli-costatum*), as in the Helianthus.

7. *Falsely ribbed* (*pseudocostatum*), is when the curved and external veins, both or either, in a reticulated leaf, become confluent into a line parallel with the margin, as in all Myrtleblooms (Myrtaceæ). This has not been before distinguished.
8. *Radiating* (*radiatum*), when several ribs radiate from the base of a reticulated leaf to its circumference, as in lobed leaves. This and the following form the *f. directè venosum* of Link: it is the *f. digitinervium* of A. Richard. Hither I refer, without distinguishing them, the *f. pedalinervia, palminervia,* and *peltinervia* of De Candolle; the differences of which do not arise out of any peculiarity in the venation, but from the particular form of the leaves themselves.
9. *Feather-veined* (*pennivenium*), when the venæ primariæ of a reticulated leaf pass in a right line from the midrib to the margin, as in Castanea. This has the same relation to the radiating leaf that the curve-veined bears to the straight-veined; it is the *folium penninervium* of De Candolle.
10. *Hidden-veined* (*introvenium*). To this I refer all leaves the veins of which are hidden from view by the parenchyma being in excess, as in Hoya, and many other

plants. Such a leaf is often inaccurately called veinless. De Candolle calls a leaf of this nature, in which the veins are dispersed through a large mass of parenchyma, as in Mesembryanthemum, *vaginervium*.

In case it should be necessary to explain the direction that the primary veins take when they diverge from the midrib, this can be denoted by measuring the angle which is formed by the midrib and the diverging vein, and can either be stated in distinct words, or by applying the following terms:—thus, if the angle formed by the divergence is between 10° and 20°, the vein may be said to be *nearly parallel* (*subparallela*); if between 20° and 40°, *diverging;* between 40° and 60°, *spreading;* between 60° and 80°, *divaricating;* between 80° and 90°, *right-angled;* between 90° and 120°, *oblique;* beyond 120°, *reflexed* (*retroflexa.*)

With regard to the *forms of leaves*, this subject properly enters into Glossology; because the terms applied by Botanists to differences in the outline of those organs are, in fact, applicable to any varieties in the figure of any other flat body. Nevertheless, as it is desirable that the student should know upon what principles the most remarkable forms of leaves, or of other divided parts, are thought to be connected with each other, the observations upon the subject made by Alphonse de Candolle, whose *Introduction to Botany* may be supposed to embody the latest opinions of his father, and by De Mercklin, who has studied the subject with more care and acuteness than anybody, are here given *in extenso*.

"Leaves," says Alphonse de Candolle, "put on a multitude of forms, depending upon the manner in which they are severally organised, especially with regard to their division and the direction of their veins. These veins being in general symmetrical on the two sides of the midrib, leaves themselves are almost always of some regular figure, as, for instance, oval, rounded, elliptical, &c. Their regularity, however, is never mathematical; and there are certain leaves, like those of the Begonia, the two sides of which are most remarkably unequal.

"Leaves are either *entire*, that is, without toothings of any

kind; or *toothed* in various ways upon their edges; or divided more or less deeply into *lobes*, which leave void spaces between them, which we call *recesses* (*sinus*.)

"Differences of this kind only become intelligible when one starts from the idea that a leaf is a mere expansion of tissue, in which the parenchyma is more or less extended, according to the divergence of the vessels that compose the veins, and to the degree of vegetating vigour of every species upon all points of its surface. In this expansion, which constitutes vegetation, it may be understood, that a cellular tissue, mingled with firm parts like veins, ought to assume, especially at the edges, very different appearances. Each vein is to be considered as surrounded with parenchyma as well as the ligneous fibres of the stem. When this parenchyma stretches a great deal between the principal veins, and unites them completely up to their extremities, the leaf is *entire*; but when the separation of the principal veins is greater, and the cellular tissue is comparatively less extended, the union of parenchyma takes place in only an imperfect manner, and thus lobes and openings are produced in the middle of the leaf, or various kinds of toothings in its circumference.

"In support of this theory, which has originated with M. De Candolle, it must be remarked that the bladders of cellular tissue have a great tendency to grow together when they come in contact in a young state. The fluids which tissue secretes are more or less viscid; the growth of the bladders in diameter causes them to press against each other; they are extremely homogeneous in different parts of the same organ; all these may be supposed to concur in producing the phenomenon of which the *grafting* of one plant upon another is the most striking example. The structure of flowers depends upon the existence of this tendency, as will be shown hereafter. With regard to leaves, Dracontium pertusum affords a verification of this theory in the irregular holes pierced through the middle of its blade between the veins. The more weak the development of this leaf has been, the larger are the holes, which, in some instances, even extend to the margin, when the leaf becomes lobed. In

this case it is difficult to deny that the parenchyma developes and combines more towards the edge of the leaf than in the centre; while, on the other hand, by a different direction and another mode of development of the parenchyma, the contrary takes place in the greater part of leaves. The fact, that divisions are the deepest in those individuals of the same species whose vegetation has been least favoured by humidity and the nature of the soil, is a confirmation of this theory.

"Palm trees seemed to offer an exception to this mode of accounting for the formation of lobes; but the recent observations of Mohl have demonstrated that those plants also are conformable to the theory. The leaves of Palm trees begin by being apparently simple, they then gradually divide from the extremity to the base of the blade, and there are on the edges of the divisions some ragged remnants, which look as if they indicated an actual rending asunder. But Mohl, by observing these leaves microscopically, when first developing, ascertained that these divisions never are intimately united at their edges, and that they are merely held together by a net of down. This may possibly depend upon the dry and leathery texture of their leaves, which causes the bladders to be converted into hairs instead of uniting in consequence of their great approximation. If the adhesion is incomplete, it is no wonder that the leaves should separate in proportion as the veins diverge by the enlargement of the leaf. Palm leaves, then, are not, as has been supposed, simple leaves which divide into lobes contrary to what happens in other plants; they are divisions bordered by a parenchyma which has never been united to that of the division next it, and which, in consequence, does not tear, but only separates.

"The unequal degrees of union of the parenchyma that surrounds the veins, combined with the arrangement of the latter, form the principles on which the nomenclature of divided leaves has been contrived.

"When the parenchyma between the primary veins is not united, so that the blade is composed of several distinct parts combined by the midrib only, the distinct portions or lobes are called *segments*. They differ from the leaflets of more compound leaves merely by the circumstance of not being

jointed with their support, nor deciduous. A leaf having such segments is called *dissected.*

"If the lobes are united near the base around the origin of these veins, we name them *partitions,* and the leaf is said to be *parted.*

"Supposing the lobes to be united as far as the middle, they become *divisions,* their recesses are *fissures,* and the adjectives formed from these are made to end in *fid,* as *multifid, quinquefid,* &c.; this should not be applied to any cases in which the divisions extend below the middle of the veins; it is, however, frequently applied to cases of a division as deep as the midrib.

"Finally, if the adhesion of the lobes is complete, and if the parenchym which separates the extremity only of the veins is not extended to the extremity of the principal veins, or beyond them, the leaf is merely toothed (*dentate*); the salient parts are *toothings.* When the *toothings* or *teeth,* are rounded, they become *crenels,* and the leaf is *crenelled* (or *crenate*). This form of leaf is not very important because it is not connected with the arrangement of the primary veins, while that of the lobes, already mentioned, always is.

"The terms that express precisely the important subdivisions of the leaf are combined with those which indicate venation. Thus a feather-veined leaf (*pennivenium*) may be either *pennatisected,* or *pennatiparted,* or *pennatifid,* according as it has segments, partitions, or fissures. In like manner a *palm-veined* leaf (this is what I call radiating, p. 267.) may be *palmatisected, palmatiparted,* or *palmatifid;* and so on.

"In like manner we say that a leaf is *trisected, trifid,* or *triparted,* when we would draw attention to the number and depth of the lobes of a leaf, rather than to the relation they bear to the veins. And, on the other hand, we may, by neglecting the number of the lobes, simply indicate their presence by saying that a leaf is *pennatilobed, palmatilobed,* and so on.

"The lobes themselves are sometimes subdivided upon the same principle as the leaf itself. We then say that a leaf is *bipennatisected, bipennatiparted,* &c.; if the subdivisions of the lobes are themselves lobed, we may say *tripennatisected,*

tripennatiparted, &c. Finally, in cases where leaves are extremely divided, and the parenchym of the ultimate ramifications of the veins does not unite and form lobes, we say, in general terms, that the leaf is *multifid, laciniated, decomposed,* or *slashed;* terms which express the appearance of a leaf, without any very precise signification."

With regard to compound leaves, their leaflets always have the primary veins running at an angle more or less acute towards the margin. "This is perfectly intelligible if we reflect that their lateral veins represent not the primary, but the secondary and tertiary veins of simple leaves, which latter are always pennated.

"The leaflets of pennated leaves are usually placed opposite each other in pairs along a common petiole. These pairs of leaves are called in Latin *juga:* thus a leaf with one pair is *unijugum;* with two pairs, *bijugum,* &c.

"Usually one of the leaflets terminates the petiole; the leaf is then *unequally pinnated* (*imparipinnatum*); but sometimes there is no odd leaflet, and the petiole ends abruptly, or in a point or tendril: this is *equally pinnated,* (*pari-pinnatum.*)

"Sometimes the leaflets themselves are subdivided (*folium bipinnatum, tripinnatum*). In this case the lateral petioles which bear the leaflets are called *partial;* and the small supports of the leaflets themselves, *stalklets* (*petiolules*)."

Such are De Candolle's ideas of the typical formation of leaves. They offer a convenient mode of studying the modifications in structure of these organs, but they are by no means confirmed by the accurate investigation of De Mercklin, who gives the following as the result of his inquiry.

"First Period.—*Birth of the Leaf considered generally.*—On stripping a leaf-bud of its leaves, the latter are found to decrease in size in proportion as you approach the centre, and at last a microscope is necessary to distinguish them. The bud ends in a round or conical projection, which has no proper envelope. This projection is called the summit of the axis (*Punctum vegetationis* of Wolff); its lower extremity is the nucleus of the bud. In some natural orders, as in Cucurbits and Crassulaceæ, the summit of the axis is reduced to

an ideal point, because the leaves or cotyledons are so close together at their base, that they absorb, as it were, its whole mass. Analogous circumstances are met with between the integuments and nucleus of the seminal bud.

The tumour of the axis is composed of a transparent greenish mass, in which can be found some scattered granules, a great quantity of cytoblasts, and lines of separation similar to the sides of cells. This mass is coloured yellow by iodine. When the tumour first appears, its surface is often furrowed, which is due to the series of cells. The extreme edge of the tumour is usually the most transparent, not only because its mass is less considerable, but because the sap contained in the last layer of cells is transparent. Under this layer the mass is more opaque, and it is principally there that the formation of the mother-cells takes place, at the expense of which the axis grows from below upwards.

Outside the centre of the top of the leafy axis, and always nearer its apex than its base, there appears a small "excentricity," which soon takes the form of a little rounded tumour, and which, in consequence of the growth of the axis, is soon clearly distinguishable from its summit. This first degree of the growth of a leaf is absolutely identical in Exogens or Endogens, and is the same for petals, stamens, and pistil.

A lateral axis, at first very like this tumour, soon becomes distinguishable from it. The lateral axis is not formed excentrically to the periphery of the top of the principal axis, but on the same plane as the latter, so that the top of the principal axis is divided by a slit into two equal portions.

The birth of the leaf, in the form of an excentricity of the axis, is distinctly seen in the embryo, where all confusion with other organs is impossible. In Ecbalium agreste the embryo globule is a cellular spherical corpuscle; at the point furthest from the micropyle there is formed a slight depression, which grows gradually larger and larger, so that the globule becomes furnished with two "excentricities," between which the depression is found. At the point diametrically opposite the hollow, and next the micropyle a little projection is formed nearly at the same time, which grows larger and

larger. The projection corresponds to the radicle; the excentricities become the cotyledons.

In those leaves, the petioles of which end in a tendril or an awn, the rudiment of this point of the petiole is always the first to appear.

As the rudimentary tumour of the growing leaf increases in size, differences characterising Monocotyledons and Dicotyledons are visible. In Monocotyledons it is generally found that for each leaf, a rim is gradually formed around the whole nucleus of the axis; this rim is a little oblique, and but slightly marked on the side opposite the point of the leaf; it increases in size by the thickening of the upper edge, at the same time that the summit of the leaf, with which it is continuous, elongates as well, so that the whole forms a sheath, closed below and open at the top.

In Dicotyledons, as a general rule, the rudimentary tumour of the leaf increases at its base without completely surrounding the stem. When the leaves are opposite, their rudiments correspond with a rim continued round the summit of the axis; from this rim arise isolated points which become determinate parts of the leaf; in this case the completely developed leaves are contiguous or grown into one another at their base. When the leaves are completely distinct the one from the other, the rim offers, even from their first appearance, contractions which correspond to the points of separation. When the leaves are whorled, there is formed around the axis a continuous circle of small tumours, each of which corresponds to the apex of a leaf.

This first form of the nascent leaf is the same for all leaves, whether simple or compound. In some orders the summit of the axis is not visible at the period of the birth of the leaves, (especially when these are opposite), and it is only at a later period, that it rises above their base to give birth to new leaves; one might be misled in this case, and suppose that the axis is composed of leaves which had grown together.

"*Formation of a Simple Entire Leaf.*—This sort of leaf

principally occurs in Monocotyledons. The lamina, ligula, petiole, and sheath, can be distinguished in it. The formation of this leaf has been already described in a general manner in what precedes. When the leaf offers the four above-mentioned parts, the apex and the lamina are formed first, then the sheath, and lastly the petiole.

The process of development is precisely the same in Dicotyledons, except for the lamina. In Monocotyledons the lamina appears from the very first, in the form of a flat expansion which afterwards rolls up: but in Dicotyledons it generally appears as a fleshy petiole, continuous with the axis.

When the vernation of the leaf-bud is duplicate, the leaves have at their first appearance, hardly any resemblance to the forms they afterwards acquire.

The plan of vernation is seen from almost the earliest period of the development of the leaves, but it is modified in many ways by subsequent developments.

In Liriodendron tulipifera for example, the youngest leaves form a semicircle on the axis; afterwards when the petiole is formed, their vernation becomes inclinative; and lastly, but before the expansion of the bud, the leaves are almost erect.

"*Formation of the Lobed or Divided Leaf.*—The apex of the leaf rises on the axis in the shape of a little tumour; other small tumours joined by a fleshy rim, are emitted right and left at the same time that the original one is being developed; new tumours join themselves to the first, so that the axis at length becomes a large lobe with five, seven, nine, or more notches; this lobe rests on a base which is more or less enlarged, or on a short thick stalk, which, if there are any stipules, is not clearly defined until after their formation.

In leaves which, when completely formed, have small lobes alternating with the large ones, the small ones are never visible at the birth of the larger, but they appear at a later period, and are developed in the same way.

On stripping a bud of Acer campestre below the outer scales, from three to five pairs of leaves almost completely

developed, are found. Subjoined is the result obtained on measuring the relative lengths of these organs.

A leaf of the	1st pair	measured	25 millim.
„	2nd	„	18 „
„	3rd	„	12 „
„	4th	„	5 „
„	5th	„	$1\frac{1}{4}$ „
„	6th	„	$\frac{1}{2}$ „

The four first pairs of leaves had already a distinct petiole; the fifth leaf was a large palmate or reniform scale, with five unequal lobes. After this a rim is found clasping the nucleus of the axis, the apex of which rises up like a small tumour. As soon as the rudimentary leaf is like a hand with five fingers, little tumours appear at the segments and are afterwards developed into small lobes. The development of the leaves of the Vine and of the Ribes takes place in the same way.

The toothings of the edge are not visible at the first appearance of the leaf.

"*Formation of Stipules.*—When the rudimentary leaf of Liriodendron tulipifera is like a small cone, there is no trace of any lateral inequality. The base of the cone is afterwards seen to extend obliquely on each side on the axis of the bud; these extensions finish by forming two projecting tumours, which cover the top of the axis in such a way that their edges touch one another on the side opposite the apex of the leaf. These two tumours are nothing but the stipules. If the entire organ is now isolated, an incompletely closed spur is obtained, the top of which corresponds with the apex and lamina of the leaf, while the edges represent the stipules; on unrolling this leaf and its stipules a lyre is obtained; the petiole being still imperceptible. The length of this rudimentary leaf is about $1\frac{1}{2}$ millimetre.

In Tilia europæa, the nascent leaf is originally applied to the axis, then it forms an ovoïd tumour which corresponds with the lamina. The edges of the latter grow obliquely upwards on the nucleus of the axis; they thus form two projecting points which grow rapidly, and eventually become

lateral lobes continuous with the lamina, which is as yet without a petiole.

In these two, as well as in all other cases, the stipules of the rudimentary leaf appear as portions of the blade; and it is not till later, in consequence of the development and elongation of the petiole, that they are at a sufficient distance to be considered as distinct organs.

In all simple leaves, stipules never appear with the first rudiments of the blade; they are developed with the lower parts of the blade which generally contain the petiole.

In compound leaves, stipules are found on the youngest part of all the leaf.

In Melianthus major, the stipules do not appear before the leaf forms a distinctly lobed organ. They are first seen as an annular rim between the axis and the base of the leaf.

In Leguminous plants (Lathyrus venosus, Pisum sativum, Medicago sativa, &c.) the stipules are originally found situated in a point nearly vertically below the top of the axis; and it is only later that they are found pushed towards the edges. All leaflets otherwise situated never become stipules. So long as the leaflets of a leaf are not evident as lobes or toothings, no trace of stipules can be found, but in time they appear on the axis as projecting points. In certain cases they do not appear, until the lobes, which eventually become leaflets, begin to form laminæ.

In Roses, no stipules appear until the leaf is sufficiently developed so as to look like a simple crenated leaf. The edges of the basal toothings extend on the periphery of the axis, they then rise into rims which become in their turn toothings and attach themselves on each side to the old ones. Later, and in consequence of the development of the petiole, these lower toothings, which are gradually being transformed into lobes, become separated from the upper ones, and it is not until then that they constitute stipules.

The leaves of Costus speciosus are composed of a blade, a short petiole, and a closed sheath, crowned on its upper edge with a membranous, lacerated pellicle analogous to a ligula. On examining its buds and removing five or six rudimentary leaves, the nucleus of the axis is found to be surrounded by

several incomplete envelopes (leaves). On removing these the nucleus of the axis appears as a naked tumour, having, at a certain period, a furrow situated nearer its periphery than its centre; behind this furrow a convex excentricity is afterwards formed. This convex part gradually rises, so that its highest point passes beyond the summit of the axis, is continued obliquely on each side on the periphery of the axis, and at last closes on the point opposite it: in this state it forms a rim clasping the axis, and continuous with the original excentricity, which now forms a boss distant from the axis, which it goes beyond. A little later the whole of this organ is distinctly furrowed, which is owing to the cells being disposed in lines. The annular rim then elongates and forms a sheath, and, at the same time, the boss is developed into a foliaceous envelope covering the axis or the less advanced leaves that are immediately continuous with the sheath. The edges of this envelope never grow together; but when they are grown so large as to touch one another, one grows beneath the other, so that the completely formed leaf is rolled spirally over the parts beneath. In this stage of the growth, the petiole exists only as an undefined mass, and the ligula is not perceptible.

In some Grasses that I have examined (as Barley and Wheat), the formation of the leaves is the same as that just described. The leaf grows in the form of a tumour, extends itself over the periphery of the nucleus of the axis, eventually surrounding it by its base, which becomes a sheath while the upper part rises obliquely on the axis. Whilst the blade of the leaf is still applied above to the top of the axis, a slight rim is formed on its inner surface, immediately above the top of the axis; the base of this rim occupies at least two-thirds of the breadth of the blade of the leaf. On isolating the blade, the rim appears as a projecting line in which series of cells can be distinguished; it is this rim that becomes the *ligula*.

My researches on this subject are too limited to enable me to decide whether the formation of the ligula is absolutely identical with that of stipules in Dicotyledons.

The conclusions to which my observations have led me,

are quite contrary to those of M. Regel (Linnæa, xvii., second part, 1843), who thinks that stipules, especially of Monocotyledons, grow before the leaves.

"*Formation of a Compound Leaf.*—The formation of compound leaves differs very much from that of simple ones. In both, however, the apex is the part first formed.

A compound leaf resembles at first a simple, sessile, undulated or crenated leaf; it then becomes lobed, then pinnatifid, and lastly pinnate.

The leaf of Baptisia minor consists of three shortly petiolate leaflets, and of two oblongo-lanceolate stipules. The summit of the axis of the leaf-bud is a roundish cone; its form is, however, considerably modified in consequence of the development of the leaves. The tumour which appears first, and which corresponds with the middle leaflet, grows from the top of the axis, so that the latter has two unequal projections separated by a slight depression. This tumour then elongates obliquely, and is by degrees changed into an ovoïd, sessile scale, surrounding nearly the whole axis, and having three bosses. The two inferior bosses, which are the smallest, are opposite to and correspond with the two lateral leaflets. The scale increases in size, and applies itself to the axis by its three bosses, which are joined by two others, the stipules; the scale now completely surrounds the axis. The bosses become more and more distinct; and we at last find a three-lobed leaf, sheathing the axis on one side, and bearing two stipules on its opposite side. All the succeeding transformations are perhaps attributable to the influence of the common petiole; for from this time forward none of the perceptible parts of the leaf are any longer in direct conjunction with the axis; between them is seen a shapeless cellular mass, which subsequently becomes the common petiole; the marginal incisions penetrate more and more into this mass, and a trifid leaf is eventually formed. The rest of the mass forms the petiole, and partial petioles.

The axis of the leaf-bud of Medicago sativa is a roundish cone. At the time that the leaves are formed we find on its periphery a little cavity above a rather rounded projection.

This projection is like a rounded tumour, and is the beginning of the apex of the terminal leaflet on the side of the axis opposite the tumour, and a little above it, an excentricity belonging to a younger leaf afterwards appears. This excentricity becomes a tumour, which lengthens more and more laterally to the axis, whilst its base increases at the expense of the latter, and from its summit to the axis, there is a projecting line terminating on each side of the periphery of the axis in a small swelling; to this swelling another springing from the axis is soon after added; a little later five toothings are seen on the edge of a large ovate leafy expansion. These toothings are nothing but the three leaflets and their two stipules, having soon after their birth the appearance of a simple crenated, and afterwards lobed leaf.

The leaves of roses when they are attached to the axis by a small base also resemble simple, oblong or ovoïd leaves, with seven or more toothings; at this stage they have no trace of either petiole or distinct leaflets.

The nascent leaflets of compound leaves are, with the exception of the terminal leaflet, symmetrically disposed on the two sides of the petiole; but when perfectly formed this symmetry is often lost.

If we compare the form of a compound leaf, when its basal leaflets and stipules have just appeared at the axis, with a young simple leaf we find no difference between them; for at this degree of development the compound leaf is nothing but a simple leaf. It is not till later, when the constituent parts are no longer in direct relation with, nor form a part of, the nucleus of the axis, that they assume a form corresponding with that of a perfectly developed leaf. It is in this, as it were, secondary formation of the parts of a compound leaf that there perhaps exists a distinctive character between it and the really simple leaf, from the number of which we must withdraw many forms which are at present referred to this class; for, as has been shown by Grisebach, many parted leaves have not in the beginning all their segments. I have not a sufficient number of observations on the development of decompound or supra-decompound leaves, to be able to enter at present into that subject.

"*Formation of the common Petiole and of partial Petioles.*—A compound leaf gradually passes from the rudimentary state, similar to a simple, crenate or lobed leaf, to the form of a perfect compound leaf. The toothings or lobes grow by their base at the expense of the common lamina, so as to form with the latter a palmate or pinnatifid leaf. The segments ultimately offer a distinctly limited base: they are more and more separated on a large petiole, to which the leaflets are attached either immediately by their base or by partial petioles. I cannot state what is the precise origin of these partial petioles; I have never been able to see them distinctly, before the lamina of the leaflets has begun to be developed. The form of the common petiole does not become distinct before the perfect development of the leaflets.

"*Formation of Stipels.*—I have only seen this formation well in Robinia hispida. When the young leaf is still like an oval oblong organ, terminating by a crenel, and having besides from eight to ten crenels on each margin, no trace of any tumour is to be found, either in the crenels or between them. But as soon as the leaf is so far advanced that the leaflets with their petiolules can be seen, and that the blades of these leaflets also begin to be manifested, then we find a little tumour at the axil of the petiolules; which tumours eventually become stipels. We may conclude with truth, from this observation, that stipels, as well as leaflets, owe their origin to the common petiole, and are formed after the leaflets. This being the case, the common petiole plays the part of an axis towards the leaflets and stipels.

The base of the common petiole of Leguminous and of some other plants often has two callosities, which are exactly where we should expect stipules to appear; these callosities ought, I think, to be considered as abortive stipules.

Second Period.—*Development of a Leaf in General.*—A growing leaf, successively produces new parts proceeding from the axis as crenels, discs, lobes or leaflets. Arrived at a certain stage, this organ undergoes no other changes than

what are owing to a growth which takes place in all directions. A considerable increase of size is the consequence, but it is not likely that this increase affects the mass in the same degree. The form of the leaf suffers considerable alterations. These changes, however, proceed in a much more rapid and uniform manner, in all the parts, than the preceding developments.

Measurements made on the increase of leaves have furnished results, which though curious can have no real value, so long as the causes of this phenomenon, and the way in which it takes place, are unknown.

The development of a leaf always begins at the oldest part of the rudimentary leaf, viz., at its apex, whence it proceeds towards its base. The development of all foliaceous organs appears to proceed in the same way in this respect; but the rapidity with which it proceeds, and the size to which it extends, vary considerably according to the situations of these organs. It is, in general, only in consequence of this development that the blade, the petiole, and other constituent parts of a leaf are formed, and consequently these organs could not have existed from the very first.

When a leaf, or certain parts of a leaf, become distinct from the axis, their immediate connection with the latter is more or less destroyed, and their respective position is changed. This takes place more especially with the apex of the leaf, which is placed the furthest from the axis. The leaf, nevertheless, still continues dependent on the axis, especially as concerns those parts which are the closest to it. Now, as it is always the base of a leaf that is in this condition, we must refer the force and rapidity of its development to this cause.

Anatomy shows us that the vascular bundles of the axis penetrate into the base of a leaf before they arrive at its apex. Moreover, liquids absorbed by the roots, penetrating the axis and lower leaves, arrive at the base sooner than at the summit of a leaf, where their constituent parts have already undergone considerable modifications.

It is on these conditions that the differences observed between the development of the lower and upper part of a

leaf, chiefly depend. The most essential of these differences are as follows:—

1st. The most considerable development of a leaf at its lower extremities. All measurements confirm this fact. I have made some observations with this end in view, on Polygonum hydropiper, the coloured spots on the leaves of which serve very well as points of comparison. The following are my results:—

1st leaf;	total length,	105	millim. ;	from base to the spot,	58	millim.
2nd „	„	98	„	„	50	„
3rd „	„	93	„	„	41	„
4th „	„	78	„	„	33	„
5th „	„	60	„	„	20	„
6th „	„	48	„	„	11	„
7th „	„	35	„	„	5½	„

The breadth of these seven leaves (which were taken from a lateral branch) immediately below the spot was, for the

1st leaf,	45	millim.	
2nd „	43	„	
3rd „	38	„	
4th „	34	„	
5th leaf,	22	millim.	
6th „	15	„	
7th „	8	„	

Consequently, the increase in length of these leaves was more considerable in their lower than in their upper half. In the first three leaves, the most considerable breadth was at the part measured, whilst in the other four the most considerable breadth was above the spot.

2nd. The generally more considerable development of the lower leaflets of compound leaves, and the slower development of the upper leaflets; the lower leaflets are also often further apart than the upper ones.

3rd. At a certain period, stipules are generally larger than the leaves or leaflets produced before them. It is only in this case that stipules can be protecting organs.

4th. The perishing of leaves from above downwards, (from apex to base.)

5th. The development of the petiole, which is analogous to that of a blade of a leaf. The outer scales of leaf-buds, which have been considered in many cases as leaves of a

particular form, are nothing but normal leaves at their birth, the lamina not having as yet been developed, whilst the petiole has taken the form of a lamina.

No direct researches have as yet been made on the influence which the vascular bundles (nervures) have on the development of the forms of leaves.

"*Development of a Simple Leaf.*—A rudimentary dicotyledonous leaf is in shape like a broad or narrow, sessile, entire, crenate or lobed scale, with or without small lobes (stipules) at its base, continuous with the lamina. Whilst the top of the leaf is distant from the axis, and the upper part of the scale is old at the same time the lower parts are still in a nascent state. The first important transformation that takes place in a rudimentary leaf is the development of the blade.

These blades may be divided into two classes. They are either developed so as to be applied by their whole surface to other parts of the bud, or they are folded outwardly or inwardly at their two halves. (*Vernatio duplicativa and replicativa.*) In the first case we see the large rim that constitutes the lamina, extend its edges more and more above the parts on which it reposes, until it envelopes them; it at the same time diminishes in thickness, the edges being the thinnest parts. There sometimes remains on its surface a projecting medial line; at other times this line disappears, leaving the lamina of nearly equal thickness throughout, as it is found in most Monocotyledons. When the edges have proceeded so far as completely to envelope the youngest parts of the bud, and to touch one another, they often grow together at their base, and folding several times, roll themselves more or less completely round the bud; whence it happens that the blade is rolled spirally, the spiral being capable of describing many turns of which the most recent are always the nearest to the axis.

In Dicotyledons convolute vernation is much more rare, for the base of the rudimentary leaf does not generally occupy the whole of the periphery of the axis. When the young foliaceous lamina of these plants is folded round the axis, it embraces it, either wholly, (by sometimes several convolutions),

or partly (half way only when the leaves are opposite), so that the internal sides of the two surfaces cover each other above the top of the axis; as for example in Bryophyllum calycinum, the Gentians, and many other species.

The most usual plan of development in Dicotyledonous plants is that in which the halves of the leaves are applied the one against the other; this plan is, however, subject to many modifications, as each half can be rolled or folded on itself, and may have transverse or longitudinal folds. That part of the leaf which resembles a rim is the first to lengthen and become thin at its edges, which turn in, and at length generally meet on the medial line of the blade. The result of this is at first a slight furrow, commencing below the apex of the leaf, and extending to its base. It is easy, at a certain period, to see that this line is formed by the approach of rims manifested at the edges of the blade, and that it is lost near the base. After a time, when the furrow is deeper, and it extends as far as the base of the blade, the two halves of the latter are sufficiently developed to touch, or every where to cover, one another.

In this plan of development, the young laminæ cover one another, either by turning their edges to the axis, (*Vernatio duplicativa*), as in Liriodendron, Leguminous plants, &c., or by turning their edges from the side opposite the axis (*Vernatio replicativa*), as in some Labiates.

The progress of the line formed by the contact of the edges of the lamina is not always equally rapid in all parts of the leaf.

The formation of a peltate leaf is owing to a very strong development of the lower part of the blade. A rudimentary leaf of Tropæolum majus resembles a five-lobed or quinquefid leaf, furnished with a short broad petiole; it is about a millimetre long. At the point where the petiole joins the lamina, *i. e.* at the edge of the latter, are two small bosses which belong to it. The bosses are the most recently developed of the whole blade; they afterwards form two small lobes; the leaf has then seven distinct lobes. All these lobes approach each other, in consequence of the development which takes place in all directions, but especially at

the base of the leaf. The lobes by degrees disappear and the leaf then has only seven slight marginal undulations. At the same time the point where the petiole and blade originally touched, is carried from the periphery to the centre, in consequence of the more considerable development of the lower half of the lamina.

The edges of a young leaf (even if it becomes perfectly entire), appear to be always more or less undulated or crenated in consequence of the cells being disposed in series, and being also spherical. When the leaf begins to fold itself, there is no trace to be found of teeth or crenels, which afterwards appear on its edges. But when the edges touch, we find projections of variable size on them, which are nothing but nascent teeth or crenels.

When a simple leaf is lobed or cut deeply at its margin, the incisions are, as I have already stated, manifest from the very beginning. There are, however, some exceptions to this rule; the small lobes of unequally lobed leaves, of Acer campestre for example, do not appear until after the formation of the larger lobes.

In Liriodendron tulipifera, that part which in the nascent leaf corresponds with the blade, resembles a subulated petiole bent upon the axis. At the time when the stipules almost completely envelope the axis, we find on the inferior surface of the lamina two very delicate lamellæ, narrowed at the base and continuous with the stipules: these are the two halves of the leafy lamina; they touch one another above, and form a double straight line which has not as yet any traces of the lobes found there at a later period. At a more advanced stage when the petiole begins to be distinguished from the blade, we find that the edge of the two lamellæ is slightly undulated. Later, lastly, the two halves are evidently lobed and applied to each other by their internal surface. The subulate body then occupies the place of the medial nervure, and its size has manifestly decreased in proportion.

The young leaf of Acer campestre has at first five crenels, and then five lobes. These lobes are cylindrical, dilated at their base; below their summit, which is obtuse, we find

depressed lines which are continued to the base, in juxtaposition with the nascent lamellæ. And the lobes do not begin to have bosses scattered over their periphery, before these lines manifest themselves on the lobes. At the same time that the lines extend on the lobes, the bosses grow and become cylindrical tumours. Their apex lastly is equally furnished with opaque lines, which indicate the formation of leafy lamellæ, which, like the large lobes, have a duplicate nervation.

Stipules of Dicotyledonous plants appear like parts of the blade of a leaf; but after a time, in consequence of their own development as well as of that of the petiole, they become distinct organs no longer having an immediate connection with the lamina. At a certain stage of their development they are larger than the leaf that gave them birth.

When stipules are first produced on the axis, they resemble, as all nascent leaves do, small tumours continuous with the leaf-like expansion. It would in many cases be difficult to decide whether they are always produced as two distinct bodies. I have generally seen them like two projections confluent at their base and embracing the axis. Sometimes (in many Papilionaceæ for example) we see clearly that they do not appear as a continuous rim, but as two small isolated tumours, which after a time either grow together at their base, or remain constantly disunited.

The lamina of a stipule is developed in precisely the same way as that of a leaf, except that instead of folding down upon itself, it extends in every direction, either immediately on the axis, enveloping it, or on the youngest parts to which it serves as a protecting envelope. The petiole, which expands principally in length, and which limits one of the sides of each stipule, is a constant check on the equilateral expansion of the blade of this organ. When this obstacle does not exist (as for example in Melianthus major and the Polygoneæ), growth takes place equally in all directions, and it then frequently happens that the points that touch grow together.

The formation of the stipules of Melianthus major has been already described. The annular rim constituting the

nascent stipules is originally completely open at the point opposite the base of a leaf, whilst it only offers a notch at the point which is applied at the base of a leaf. This notch becomes an incision by the growth of the edges, which terminate in points, at the same time that the rest of the rim rises on the axis; nevertheless remaining open on one side. An envelope, which finally completely covers the axis, is the result, the incision remaining always, whilst the open side is closed in consequence of the growing together of the edges. These stipules, called interpetiolar, are placed between the petiole and the axis; they completely envelope, during a certain time, the axis and the less advanced leaves.

The transformations of the *petiole* caused by its development are of little importance, in consequence of the uniformity of this organ, and of its extension taking place almost entirely in a longitudinal direction. In a nascent leaf the petiole is generally of no distinct form, and even when it exists from almost the very beginning, it is very ill-defined compared with what it subsequently becomes. Measurements have proved that its principal development is from above downwards. Its development modifies very considerably the position of the stipules relatively to the blade of the leaf. Stipules are originally inserted on the petiole along the whole of their inner side, whilst their outer side is applied to the axis, and their base in common with the petiole springs from the axis. Now, the extension of the petiole taking place principally at its summit, the blade of the leaf is separated more and more from the stipules, the base of which is in no way displaced; and the more the petiole raises the blade, the further the latter gets from the stipules, which finally become totally distinct organs. This is very striking in Liriodendron tulipifera. The leaf, including the stipules of this plant, is originally nearly lyrate, with a large opaque line where the midrib is afterwards found. A portion of the petiole about half a millimetre long, afterwards appears at the spot where the furrow is deepest, and separates the edge of the lamina from that of the stipules. When, however, the leaf is completely formed, the length of the petiole is at least sixty-five millimetres.

"*Development of a Compound Leaf.*—A compound leaf, when its leaflets and stipules become first visible, is like a crenate or lobed leaf, inserted on the axis by a base more or less enlarged. As the crenels or lobes which correspond with the leaflets are no longer in direct relation with the axis of the bud, from which they are separated by the rim, which is in the place of a common lamina, it is probably in this lamina that the mother-cells are formed, which serve for the growth of the crenels. The latter gradually become leaflets. Whilst this transformation is going on, the leaf, which was at first simple, becomes lobed, then pinnatifid, then pinnate, then, and not before, the leaflets begin to be developed; they behave with respect to the rachis, as the originally simple leaf did with respect to the principal axis.

The blade of the leaf is first formed, and moreover in such a way, that the young lamellæ fold up so as to produce a medial furrow, extending from their apex to their base. This is the only mode of development found in really compound leaves. As to the stipules, if they remain immediately next the axis, they extend their blade over its nucleus (as for example in Baptisia minor and Melianthus major), and this is the real difference between them and leaflets.

When the blade of the leaflet is tolerably advanced in its development, the petiolule begins to appear, either as a contraction, or as a small cylindrical stalk; from this time forward the development of the leaflet is no more retarded.

When there are any stipels, their development begins at the same time as that of the partial petioles. Their symmetrical development is often interfered with by their position relative to the petiole and partial petioles; whence they are often abortive, or they are only developed as prickles or very narrow leaflets.

The most remarkable change to which a compound leaf is subject is caused by the development of the common petiole. Whilst the leaflets become more and more distinct, as lobes or crenels of the lamina, the remaining portion of the latter organ constitutes an elongated and more or less cylindrical body, proceeding from the nucleus of the axis, and supporting the leaflets. In other cases a very short stem only

remains after the birth of the leaflets, and the latter are then originally inserted immediately on the axis.

It seems from what precedes that the plan of development of a compound leaf is generally the same as that of a simple one, that is to say, it proceeds from the apex to the base. But the longer the common petiole, the greater the differences between the upper and lower parts; and the latter although last formed, are often much more considerably developed than the former. Yet some observers, and especially Steinheil, have drawn from this fact a conclusion as to the origin of these parts that is entirely unwarrantable.

Each leaflet considered by itself is also developed from above downwards; but its stipels do not proceed as the stipules of a simple leaf. In the small number of cases in which I have observed these stipels, they have never been developed before the leaflets accompanying them; moreover they are not produced, like stipules, as parts of the lamina of the leaflet, but as small tumours at the base of the partial petiole.

A very young leaf (about $1\frac{1}{2}$ millimetre long) of Melianthus major is composed of a palmate blade with five, seven, or nine lobes of various lengths. The lamina has as yet no petiole, and is applied at its base against the axis, from which, however, it is separated by the interpetiolar stipule which already exists as a rim. The three terminal lobes of the leaf are considerably larger than the lower lobes. All these lobes cross at their base, and they consequently penetrate further and further into the lamina, whence results a five-parted leaf, three or four millimetres long. Later, an opaque line is found on the anterior surface of the terminal lobe, which is gradually extended to its base; a little while after, the other lobes offer the same formation, which is, as we know from what has already been stated, due to the development of the lamina of the leaf. At the same time, the bases of the leaflets, which were originally arranged almost in a semicircle, separate more and more, so as to form a lower and an upper pair, and a terminal leaflet; they have all a short broad stalk, continuous with the medial line of the terminal leaflet; the total length of the leaf is at about this time from six to seven millimetres; it already represents, on

a small scale, the perfectly developed leaf, the length of which is from 150 to 200 millimetres. The leaflets then acquire, in the way above described, their leafy halves. The short broad petiole lengthens rapidly, and at the same time there appears immediately below, but only on one side of each leaflet, a thickening which is continuous with the edge of the leaflet, forming at first an unequal rim, and afterwards a small dentate leafy blade, continuous with the lamina of the leaflet. It is this that constitutes the winged petiole.

The formation of the lamina of Papilionaceæ is tolerably alike in all the species that I have examined. The leaflets are folded so as to form a duplicate vernation. The leaflet, at first doubly convex, is hollowed or flattened on the side that afterwards forms the upper or under surface; its edges are raised in the shape of a rim, which gradually spreads on the concave part in which the midrib is afterwards formed. When they touch each other on the medial line, they form a deep opaque furrow, situated between two projecting ridges, which become gradually thinner, and ultimately form the leafy lamellæ.

"*History of the Development of the Leaves of* Ceratophyllum demersum.—The axis of the leaf-bud is a rounded cone, having below its summit a great quantity of nascent whorls, of which the upper are completely covered by the lower. There is no whorl immediately below the top of the axis; not far below it we, however, find two or three indistinct rings; a little lower still, we see several whorls of contiguous little tumours; and below these again, several crowns formed by little straight points are observed. The whorls are separated from each other by small portions of the axis, which are either naked or covered with the rudiments of leaves. The interstices are smaller near the top than near the bottom of the axis.

The number of leaves of which a complete whorl is formed varies from ten to sixteen. It is almost impossible to count the exact number of little projections in the nascent whorls; there are often from thirty to forty of them. These nascent whorls bear a great resemblance to the integument of an ovule, when being formed.

The form of the leaves composing the first distinct whorls, is that of a rounded and nearly plane crenel. One of the whorls, if isolated, looks like a ring deeply crenate on its upper edge; each crenel corresponds with a bifurcation of the perfect leaf. All these crenels are originally equal in size, and joined together in pairs, or in fours at their base: the incisions never penetrate as far as the base of the leaves.

The succeeding transformations are caused by the crenels becoming a little pointed and unequal, at the same time that the incisions penetrate further into the common base, whence results a four-cleft palmate scale, the lobes of which are of unequal length. This form is already tolerably like that of the completely developed leaf. After a time the scale grows principally in length: the four points are more distinctly separated, the middle ones always remain the longest, their edges become covered with peculiar tumours, their summit is crowned with a cellular appendage, and lastly the leaf, originally quadricrenate, becomes dichotomous.

The cellular appendage found at the top of each fork merits some detail. From the time that each point of the fork is a rounded crenel, the extremity is found to be composed of five, six, or more, very small transparent cells, whilst the rest of the mass is opaque, yellowish, and without distinct cellular sides. In proportion as the crenels grow larger, the cellules at the top also become larger, and several other similar cells are added to them; they are all placed on the immediate limit of the edge. These cellules afterwards distinctly project beyond the edge; the terminal ones increase in number, and form a string of three or four series, terminated by one solitary cellule, and lying on a base of several more transparent cellules. This thread acquires its greatest vigour on leaves that are almost completely formed; it then becomes attenuated into a brownish thread, and disappears altogether when the leaf is in its last stage of development. The cellules of this string are oblong oval, translucent, and filled with whitish, transparent, irregularly shaped corpuscles, which appear to be grains of starch, but may possibly be cytoblasts beginning to be dissolved. This string, looking at the way in which it is formed, and its short duration, may be compared

with the hairs that are formed on young leaves; it is therefore no exception to the general rule that leaves grow by their base.

"*Formation of the Leaves of* Amicia Zygomeris, D. C.—The axis of the leaf-bud is originally shaped like a conical tumour that afterwards bccomes a cylinder with a large base, and a convex projecting apex. A little below the top, there appears a small excentricity, which gradually becomes a tumour, and is turned off nearly horizontally from the top of the axis. The base of the tumour extends a little on the periphery of the axis, at the same time that its summit is raised, and passes beyond it.

In a short time, the tumour becomes a fleshy, expanded scale, with three bosses, of which one, the oldest and largest, is terminal, whilst the other two are still continuous with the axis. At this time a line drawn across the axis to the top of the scale, was found to be $\frac{7}{80}$ to $\frac{9}{80}$ lines long; about one half of this length belongs to the diameter of the axis, so that the length of the leaf at this stage of its development, can be estimated at $\frac{1}{20}$ lines. Two other bosses are afterwards formed on the axis, one on each side; the scale is then a simple, convex leaf, with five unequal bosses; the terminal boss corresponds with the point of the common petiole, the four others become leaflets. The leaf in this imperfect state, undergoes many other transformations. It is remarkable that the terminal boss, originally the largest, is gradually absorbed, as it were, by the developing leaflets.

At the same time that the tumour, corresponding with the point of the common petiole, is formed on the nucleus of the axis, we find round the latter a slight rim, below, and having no connexion with the petiolar tumour. Another rim, on the opposite side of the axis, corresponds with the former one; they are both at first quite distinct from each other, but they soon approach and unite by their lower edges, whilst they remain constantly free above. The two points of contact always meet on the same points of the periphery of the axis, because each of the two rims occupies half of the surface of the nucleus. One of these points is placed

immediately below the base of the leaf, the other is directly opposite this base. These rims afterwards become semicircular, convexo-concave valves, enveloping the axis and touching each other at their edges; they then form the organs considered as stipules; but they are never in organic connection either with the leaflets, or with the petiole, which is contrary to what is generally observed in stipules of compound leaves.

"*Conclusion.*—The way in which I am led from the above facts to regard the formation of leaves is shortly as follows:—

All leaves are produced on an axis, and their first form is that of a tumour. The lobes, segments, or leaflets on the lower half of a completely formed leaf, are produced from the axis, after the lobes, segments, or leaflets on the upper half.

The original tumour corresponds with the apex of the leaf, or with the summit of the common petiole.

In all leaves, the blade and top of the petiole are formed before the stipules and the lower part of the petiole.

The formation of compound leaves consists of two stages; first, that of a simple leaf; then that of a pinnate leaf. It is not very probable that the second owes its origin to the axis of the leaf bud as the first does.

The petiole (either of a simple or of a compound leaf) ought, whether we regard its position relative to the axis or its anatomical structure, to be considered as an immediate elongation of the axis; it certainly has a great influence on the formation of the leaf.

The stipel is formed after the point of the leaflet which it accompanies; its development is generally much slower than that of a stipule.

All the parts of a leaf are symmetrical from their birth, and the rudiment of each leaf is a body symmetrical in its relation to the axis.

The young leaflets of all compound leaves, are always opposite.

All the parts of a rudimentary leaf are capable of development. This development generally proceeds from the apex to the base of the leaf, and is greater and stronger towards

the latter. The development takes place in all directions, and predominates in determinate directions.

The blade of a leaf is first developed. Leafy lamellæ are extensions of it, whether they are equilateral or inequilateral.

Teeth and crenels appear to be owing to the development of certain series of cellules from the edge of a leaf. No trace of them is to be found in very young leaves, the blades of which are beginning to be formed.

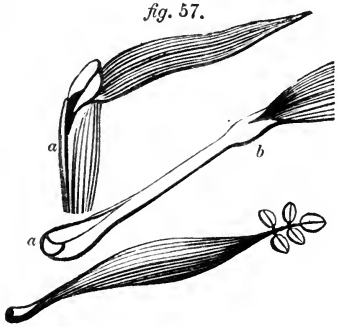
Stipules of Dicotyledons, in consequence of the great longitudinal development of the petiole, appear as organs distinct from the blade. The rapidity of their development is probably due to their proximity to the axis. Their blade is developed, covering the axis or other organs.

The petiole is principally developed in one direction; of all the parts of a leaf, it is that which grows the most in proportion to its original size.

Although most of these views are founded on facts, yet they want an absolutely certain basis, which cannot be obtained without observing the internal life of the parenchyma of the leaf and of its products. This ought to remain the object of a true history of the development of leaves; for at present their successive transformations only, have been observed."—(*Annales des Sciences*).

The PETIOLE, or leafstalk (*fig.* 57., *a*—*b*), is what connects

fig. 57.



the blade with the stem, of which it was considered by Linnæus as a part. It consists of one or more bundles of fibro-vascular tissue surrounded by cellular substance. It has

exactly the same physiological value as the leaf itself. Its figure is generally half cylindrical, frequently channelled on the surface presented to the heavens; but in some monocotyledonous plants it is perfectly cylindrical, and in others it is a thin leafy expansion, called the *sheath,* or *vagina,* surrounding the stem (*fig.* 57. *a*). If the petiole is entirely absent, which is often the case, the leaf is then said to be *sessile.* Generally the petiole is simple, and continuous with the axis of the leaf; sometimes it is divided into several parts, each bearing a separate leaf or *leaflet* (*foliolum*): in such cases it is said to be compound; each of the stalks of the leaflets being called *petiolules* or *stalklets* (*ramastra,* Jungius). In some leaves the petiole is continuous with the axis of the lamina, from which it never separates; in others the petiole is articulated with each stalklet; so that, when the leaf perishes, it separates into as many portions as there are leaflets, as in the Sensitive Plant. When an apparently simple leaf is found to be articulated with its petiole, as in the Orange, such a leaf is not to be considered simple, but as the terminal leaflet of a pinnated leaf, of which the lateral leaflets are not developed. This is an important difference, and must be borne constantly in mind by those engaged in the investigation of natural affinities.

At the base of the petiole, where it joins the stem, and upon its lower surface, the cellular tissue increases in quantity, and produces a protuberance or gibbosity, which Ruellius, and after him Link, called the *pulvinus,* and De Candolle *coussinet* (*fig.* 57. *a*). At the opposite extremity of the petiole, where it is connected with the lamina, a similar swelling is often remarkable, as in Sterculia, Mimosa sensitiva, and others: this is called the *struma,* or, by the French, *bourrelet,* (*fig.* 57. *b*).

Occasionally the petiole embraces the branch from which it springs, and in such case is said to be *sheathing;* and is even called a *sheath,* or *vagina,* as in grasses (*fig.* 57. *a*). When the lower part only of the petiole is sheathing, as in Apiaceæ, that part is sometimes called the *pericladium.* In grasses there is a peculiar membranous process at the top of the sheath, between it and the blade, which has received the

name of *ligula* (*fig.* 57. *b.*); for the nature of this process see page 278. In the Asparagus, the petiole has the form of a small sheath, is destitute of blade, and surrounds the base of certain small branches having the appearance of leaves; such a petiole has been named *hypophylium* by Link. In Trapa natans, Pontedera crassipes, and other plants, the petiole is excessively dilated by air, and acts as a bladder to float the leaves; except being thus in a state of dilatation, it does not differ from common petioles: it has, nevertheless, received the name of *vesicula* from De Candolle, who considers it the same as the bladdery expansions of Fuci. The petiole is generally straight: occasionally it becomes rigid and twisted, so that the plant can climb by it. In Combretum it hardens, curves backwards, loses its blade, and by degrees becomes an exceedingly hard durable hook, by means of which that plant is able to raise itself upon the branches of the trees in its vicinity.

When the petiole grows *upon* the angles of the stem it is called by Link *p. synedrus;* when between them, *p. cathedrus.*

It has been said that the figure of the petiole usually approaches more or less closely to the cylindrical: this, however, is not always the case. In many plants, especially of an herbaceous habit, it is very thin, with foliaceous margins; it is then called *winged.* There are, moreover, certain leafless plants, as some Woodsorrels (Oxalis) and the greater number of species of Acacia, in which the petiole becomes so much developed as to assume the appearance of a leaf, all the functions of which it performs. Petioles of this nature have received the name of *Phyllodes* (*fig.* 57. *c*). They may always be distinguished from true leaves by the following characters: —1. If observed when the plant is very young, they will be found to bear leaflets. 2. Both their surfaces are alike. 3. They very generally present their margins to the earth and heavens,—not their surfaces. 4. They are always straight-veined; and, as they only occur among dicotyledonous plants which have reticulated leaves, this peculiarity alone will characterise them.

But, besides the curious transformation undergone by the petiole when it becomes a phyllode, there are others still more

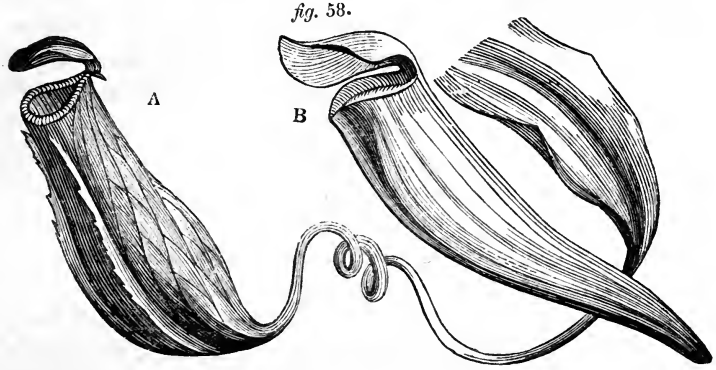
remarkable: among these the first to be noticed is the *cirrhus* or *tendril* (*Capreolus* and *Clavicula* of the old botanists.) It is one of the contrivances employed by nature to support plants by aid of others stronger than themselves. It was included by Linnæus among what he called *fulcra;* and has generally, even by very recent writers, been spoken of as a peculiar organ. But, as it is manifestly in most cases a particular form of the petiole, I see no reason for regarding it in any other light. It may, indeed, be a modification of the inflorescence, as in the Vine; but this is an exception, showing, not that the cirrhus is not a modification of the petiole, but that any part may become cirrhose.

In some cases the petiole of a compound leaf is lengthened, branched, and endowed with the power of twisting round any small body that is near it, as in the Pea: it then becomes what is called a *cirrhus petiolaris.* At other times, it branches off on each side at its base below the lamina into a twisting ramification, as in Smilax horrida; when it is called a *cirrhus pedunculares.* Or it passes, in the form of midrib, beyond the apex of a single leaf, twisting and carrying with it a portion of the parenchym, as in Gloriosa superba; when it is said to be a *cirrhus foliaris.* De Candolle also refers to tendrils the acuminate, or rather caudate, divisions of the corolla of Strophanthus, under the name of *cirrhi corollares.*

As another modification of the petiole, I am disposed to consider with Link (*Elem.* 202.) the singular form of leaf in Sarracenia and Nepenthes (*fig.* 58.), which has been called a *pitcher* (*Ascidium, Vasculum*). This consists of a fistular green body, occupying the place, and performing the functions of a leaf, and closed at its extremity by a lid, termed the *operculum.* The pitcher, or fistular part, is the petiole, and the operculum the blade of a leaf in an extraordinary state of transformation. This is found, by a comparison of Nepenthes and Sarracenia with Dionæa muscipula; in that plant the leaf consists of a broad-winged petiole, articulated with a collapsing blade, the margins of which are pectinate and inflexed. We may either suppose the broad-winged petiole to collapse, and that its margins, when they meet, cohere, in

which case there would then be formed a fistular body like the pitcher of Sarracenia (*fig.* 58. B), and there would be no

fig. 58.



difficulty in identifying the acknowledged blade of the one with the operculum of the other, or we may suppose this sort of pitcher to be in reality a petiole hollowed out near its extremity; and this idea is perhaps more conformable to known facts, especially to the circumstance figured by Korthals in the *Verhandelingen over de Naturlijke Geschiedenis der Nederlandsche bezittingen* of the very earliest leaves of seedling plants of his Nepenthes phyllamphora assuming the condition of complete pitchers. Moreover, no transitions from flat leaves to the hollow pitchers have yet been seen. I should also remark that the following passage in Mr. Low's *Sarawak* confirms the statement made by Korthals, with an important addition. "The old stems of Nepenthes ampullacea falling from the trees, become covered in a short time with leaves and vegetable matter, which form a coating of earth about them; they then throw out shoots which become in time new plants; but apparently the first attempts to form the leaf are futile, and become only pitchers, which, as the petioles are closely imbricated, form a dense mass, and frequently cover the ground as with a carpet of these curious formations. As it continues growing and endeavouring to become a plant, the laminæ of the leaves gradually appear, small at first, but every new one increasing in size, until finally the blades of the leaves are perfect, and the pitchers,

which, as the leaves developed themselves, have become gradually smaller on each new leaf, finally disappear altogether when the plant climbs into the trees. This formation of the pitcher may afford an instructive lesson to the naturalist, as, though not to the same extent, the principle is perceptible in all of this curious tribe, the leaves of seedlings and weak plants always producing the largest pitchers."

Professor Morren has, however, expressed a different opinion respecting these pitchers. He considers the cuculliform pitcher of plants as a variation in form of the blade of the leaf. "The leaf coheres by its margins, and above, absolutely as in the formation of carpels, which made me say [formerly] that the ascidium is a tendency to the floral form. Since this period new facts have confirmed the theory. During my stay at Newcastle, in Northumberland, at the meeting of the British Association, I had an opportunity of studying the different preparations of monstrosities which the Rev. W. Hincks of York, known by his 'Monograph of the Œnotheræ,' had brought there. Amongst these specimens were two of the most remarkable accidental ascidia, which permit us to classify these extraordinary deviations. One was on a specimen of Tulipa gesneriana. The leaf which, as is well known, sheaths the peduncle in this plant, had cohered at its free margins along its whole length, so that the outer surface of the pitcher thus formed was always the under surface of the leaf. But it resulted also from the complete cohesion of the margins of this organ that no aperture allowed of any communication between the outward air and that inclosed in its cavity. Nevertheless a flower and its peduncle were inclosed in this cavity, and the perianth was not less finely coloured through this envelope than are the petals of Papaver rhœas under the thick tunics of their caducous calyx. As the flower developed, it was necessary that the peduncle should grow larger, which it did to a greater degree than the ascidimorphous leaf, which remained small; but then it was also necessary that the peduncle should twist itself, or that the ascidium should burst. The peduncle prevailed, and the ascidium opened; but not as would have been supposed, by a longitudinal rupture occasioned

by a dislocation of the cohering margins, but by another very curious way of dehiscence. The ascidium formed an elongated bag, tumid in the middle, tapering at its two extremities, above and below; now this bag was split across with a horizontal rupture, just as in the ascidium the lid is detached from the pitcher, or rather as in mosses the calyptra falls off from the urn. The flower indeed carried this cap with it, and could not rid itself of it, so that the perianth remained curled up beneath and within. At sight of this tulip, having at its base a conical foliaceous hollow body, from the centre of which arose a long peduncle, terminating in its turn in an another cone, which disclosed the organs of fecundation, I could not help comparing it to a large moss armed with its calyptra. In Nepenthes and Sarracenia the ascidia also are at first shut up, and at Edinburgh, upon the beautiful plants of Nepenthes, cultivated with so much skill by Mr. Mac Nab, I was able to learn how their dehiscence takes place. The part which the circular struma acts, with its numerous small transverse ribs, then becomes very easy to understand. Before the operculum is detached, its thin margins are folded round this struma, which holds them very strongly fixed, as a bladder is fastened over the opening of a vessel by the infected margin.

"When once the operculum is freed it cannot again fasten itself above the struma. This dehiscence of the lid is therefore horizontal, or in a small degree oblique, like the direction of the struma itself, and it is nearly the same in all ascidia. On that of the tulip formed by monstrosity, the opening, although in this case it was an actual rupture caused by internal violence, took place, notwithstanding, in the same manner. This comparison deserves some attention, especially if further observations tend to confirm it."—(*Annals of Natural History*, III. 411.)

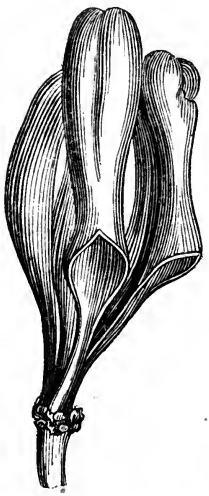
To me this explanation is not entirely satisfactory, nor do I believe that the pitchers of Sarracenia and Nepenthes (*fig.* 58 A), have any analogy with the pitcher-like expansions which frequently rise up from the surface of Cabbage leaves, an example of which is figured in the *Transactions of the Horticultural Society*, vol. V., t. 1.

The student must not, however, suppose that all pitchers are petioles, because those of Nepenthes and Sarracenia are so. Those of the curious Dischidia Rafflesiana (*fig.* 59.),

fig. 59.

figured by Wallich in his *Plantæ Asiaticæ Rariores,* are leaves, the margins of which are united. The pitchers of

fig. 60.



Marcgraavia and Norantea (*fig.* 60.) are bracts in the same state.

Spines of the leaves are formed either by lengthening of

the woody tissue of the veins, or by a contraction of the parenchym of the leaves: in the former case they project beyond the surface or margin of the leaf, as in many Solana and the Holly (Ilex aquifolium): in the latter they are the veins themselves become hardened, as in the spiny petiole of many Leguminous plants. So strong is the tendency in some plants to assume a spiny state, that in a species of Prosopis from Chili, of which I have a living specimen now before me, half the leaflets of its bipinnate leaves have the upper half converted into spines.

The production of spines by hardening veins in the absence of the usual web of parenchym, is a well known occurrence in the Barberry and Gooseberry, whose so-called spines are really nothing but spiny webless leaves. This is still more remarkable in the Puya heterophylla, which bears two kind of leaves having scarcely any resemblance to each other. Those at the base of the plant arise from tough, concave, broad, horny petioles, which overlie each other, forming a kind of bulb, and are extended into narrow, hard, serrated, spiny, brown processes about two inches long. The leaves, on the other hand, which are last formed, are thin, lanceolate, bright green, and more than eighteen inches long when full grown, and bear no resemblance to the first. The flowers are arranged in a close, oblong spike, composed of imbricated woolly cartilaginous pale green bracts, occupying the centre of a bulb of spiny leaves in the place of the thin leaves before mentioned.

Unusual forms of leaves are not, however, caused exclusively by the circumstances above mentioned. Without any peculiar enlargement of the petiole, or the formation of pitchers, or the excessive development of spiny processes, leaves of a very unusual nature sometimes occur; an example of which (the more interesting because of its frequency) is found among Conifers, which are thus described by Link in that author's admirable *Icones Selectæ. Anatomiæ Botanicæ*, Part ii. tab. 5, (1840). The leaves of Conifers are principally distinguished by having only one simple (occasionally, perhaps double) fibro-vascular bundle, which runs longitudinally

through the leaf, without throwing off side branches. What botanists call *folium acerosum* might be characterised by this circumstance alone. They also have, in most cases, one or two resinous canals, which run through the leaf from end to end; the leaves of Abies balsamea have such canals near the edge. Those of Thuja occidentalis and Juniperus communis have but one below the principal nervure. Many have a double layer of epidermal cells, as Abies balsamea, and Juniperus Sabina, the cells beneath which are also lengthened laterally, as in some Proteads. In these cases we have a leaf possessing great permanence, and a very high power of vitality, reduced to a cylinder or plate of parenchym, one single fibro-vascular bundle, and a canal to receive the secretions as they form in the leaf. From such a leaf it is easy to pass to the more complicated structure of ordinary foliage.

Some plants produce FALSE LEAVES instead of real ones. Such leaves are always modified branches. They occur in the Asparagus, the Furze, some Colletias, where they are commonly mistaken for leaves, the functions of which they certainly perform, and in various other instances. Among Indian Figs (Cactaceæ), they are often thin, flat, crenated plates, jointed end to end; in some Spurgeworts (Euphorbiaceæ) as Xylophylla, they are lanceolate, serrated, hard, straight-veined blades. These false leaves are known by several characters.

1. They proceed from the axil of a rudimentary leaf.

2. They bear leaves, or at least flowers, at their notches, whence also they emit fresh shoots.

3. The veins which run from the midrib to the marginal notches *terminate* in the *axil of the notch, and not at its point as in true leaves.*

Zuccarini gives the following account of them in Phyllocladus, a genus of Australian Conifers, (*Ray Reports*, p. 37).

"In Phyllocladus, true leaves are entirely wanting, their place being supplied merely by scales of buds or foliaceous twigs. The principal axis of the stem, or of the branch of this plant, produces buds with scales, which are either narrow and linear, or acicular, membranous, and expanding. They

are disposed on the axis at regular distances, supply the place of leaves, and usually bear no buds in their axils, but wither early. The three or five uppermost scales alone, on the extremity of each annual shoot, are crowded into a circle, and bear, each in its axil, a foliaceous twig. These twigs are articulated at the base like leaves. They are furnished with minute, distichous, alternate, remote, decurrent scales, of which in young plants from ten to twelve, but in older ones frequently, only four or five occur on each twig. From the axil of each of these scales issues a flattened, and irregularly divided twig, which approaches in its nature to a leaf, inasmuch as the under surface only, or that which looks towards the earth, is furnished with numerous stomates, whilst the upper surface is green and without stomates. In plants of older growth, the scales, from the axils of which these false leaves arise, ascend and are united to the edge of the latter, appearing at first sight to constitute merely its lowermost segment. Lastly, the branch terminates at the apex, in a false leaf similar to the rest, thus becoming as it were a complete leaf, which also in due season falls off, like those below it, and then leaves behind a permanent true axis, from which, in the succeeding year, a whorl of similar leafy branches is to be produced. For figures to illustrate this, see *Ray Reports*, 1845, as above quoted.

2. Of Stipules.

At the base of the petiole, on each side, is frequently seated a small appendage, most commonly of a texture less firm than the petiole, and having a tapering termination. These two appendages are called *stipules*. They either adhere to the base of the petiole or are separate;—they either endure as long as the leaf, or fall off before it;—they are membranous, leathery, or spiny;—finally, they are entire or laciniated. By Link they have been called *Paraphyllia*, and defined as "foliaceous parts, in structure like the leaves, and developed before those organs."

When they are membranous, and surround the stem like a sheath, cohering by their anterior margins, as in

Polygonum (*fig.* 61. *a*), they have been termed *ochrea* by Willdenow. In pinnated leaves there is often a pair of

fig. 61.

stipules at the base of each leaflet, as well as two at the base of the common petiole: stipules, under such circumstances, are called *stipels*.

What stipules really are has been a matter of doubt. De Candolle seems, from some expressions in his *Organographie*, to have suspected their analogy with leaves; while, in other places in the same work, it may be collected that he rather considered them special organs. I have always been of opinion that, notwithstanding the difference in their appearance, they are really accessory leaves: first, because they are occasionally transformed, in Rosa bracteata, into pinnated leaves; secondly, because they are often undistinguishable from leaves, of which they obviously perform all the functions, as in Lathyrus, Lotus, and many other Leguminous plants: and, finally, because there are cases in which buds develope in their axils, as in Salix, a property peculiar to leaves and their modifications. This view has been confirmed by the researches of De Mercklin as given in previous pages.

Among Cucurbits exist, in the place of stipules, processes having the appearance of tendrils, which De Candolle, after Seringe, supposed them to be. The Bravais' have suggested that these tendrils are rather to be regarded as accessory buds, (*Annales des Sciences*, 2 s. viii. 20.) But according to Payer, they are the lateral ribs of the true leaf, upon which

supposition the leaves of Cucurbits must be regarded as being compound. Mr. Payer puts the case of Cucurbits thus:—"There are many plants in which fibro-vascular bundles are detached at three different points of the circumference of the cylinder constituting the medullary sheath, generally at one and the same height, and at a little distance from the origin of a leaf: these bundles traverse the herbaceous envelope, and pass into the *pulvinus* (coussinet) of that leaf. There, sometimes, all three enter the petiole, sometimes only one of them, viz., that in the centre; the two lateral ones continuing the nervation of the two lateral stipules. Now if the lower leaves of the cultivated melon be examined, no tendril will be found to exist at their side; it will be seen that the three fibro-vascular bundles which separate from the medullary sheath, ascend all three into the petiole, and that the bud formed at their axil, and always placed between the intermediary bundle and the stem, is decidedly at the middle of the base of the leaf. If, on the contrary, the stem-leaves which have a lateral tendril are considered, we observe that of the three fibro-vascular bundles, only two, the central, and one of the lateral ones, enter the petiole, and that the other penetrates into the tendril. In this case, the bud, from its constant position between the middle bundle and the stem, is no longer, like this middle bundle, at the centre of the base of the petiole, but on the side, and appears to be almost between the leaf and the tendril. Lastly, we frequently meet in botanical gardens with the upper leaves each accompanied by two lateral tendrils. Anatomy then shows that a single central bundle traverses the petiole, and that the two lateral ones pass each into a tendril. With respect to the bud, it necessarily is situated between the middle of the base of the petiole and the stem." (*Annals of Natural History*, xvi. 70.)

Sometimes it is difficult to distinguish from true stipules certain membranous expansions, or ciliæ, or glandular appendages of the margin of the base of the petiole, such as are found in Crowfoots (Ranunculaceæ), Dogbanes (Apocynaceæ), Umbellifers, and many other plants. In these cases the real nature of the parts is only to be collected from analogy, and

by comparing them with the same part differently modified in neighbouring species.

Link regards the scales of leaf-buds (called by him *tegmenta*) as a kind of stipule, and such they, no doubt, sometimes are, as in the Tulip Tree (Liriodendron); but then he unites with them the primordial ramentaceous leaves of Pinus, which have no analogy with stipules.

De Candolle remarks, that no monocotyledonous plants have stipules; but they certainly exist, at least in Naiads and Arads. It is also said that they do not occur in the embryo; but then there are some exceptions to this statement, as well as to Miquel's remark, that they never occur upon radical leaves, *e. g.* Strawberry.

Turpin considers them of two kinds.

1. Distinct, but rudimentary—*Leaves*—when they originate from the stem itself, as in Cinchonads, &c.

2. *Leaflets* of a pinnated leaf, when they adhere to the leaf-stalk, as in Roses, &c.

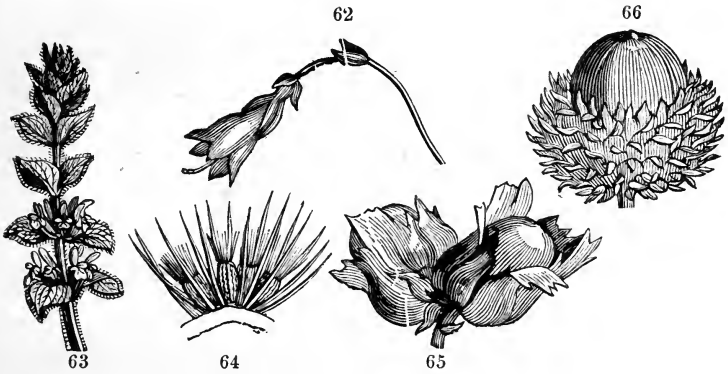
The *ligula* of grasses, at the apex of their sheathing petiole, a membranous appendage, which some have considered stipulary, should rather be considered an expansion analogous to the corona of some Cloveworts (Caryophyllaceæ). Of this the fibrous sheath at the base of the leaves of Palms, called *reticulum* by some, may possibly be a modification.

It has been already noted, that when stipules surround the stem of a plant they become an *ochrea;* in this case their anterior and posterior margins are united by cohesion; a property which they possess in common with all modifications of leaves, and of which different instances may be pointed out in Magnoliads, where the back margins only cohere, in certain Cinchonads, in which the anterior margins of the stipules of opposite leaves are united, and in many other plants.

3. Of Bracts.

All the parts hitherto made the subject of inquiry are called *organs of vegetation;* their duty being exclusively to perform the office of nutrition in the vegetable economy. Those which

are about to be mentioned are called *organs of fructification*; their office being to reproduce the species by a process in



some respects analogous to that which takes place in the animal kingdom. The latter are, however, all modifications of the former, as will hereafter be seen, and as the subject of this division is in itself a kind of proof; bracts not being exactly either organs of vegetation or reproduction, but between the two.

Some botanists call *Bracts* either the leaf from the axil of which a flower is developed, such as we find in Veronica agrestis; or else all those leaves which are found upon the inflorescence, and are situated between the true leaves and the calyx. Others refuse the name of Bract to any organs except such as are manifestly dissimilar to the ordinary foliage; and this is the common practice: mere leaves, to which flowers are axillary, being called *floral leaves*. There are, in reality, no exact limits between bracts and common leaves; but in general the former may be known by their situation immediately below the calyx, by their smaller size, difference of outline, colour, and other marks. They are often entire, however much the leaves may be divided; frequently scariose, either wholly or in part; sometimes deciduous before the flowers expand; rarely very much dilated, as in the Dittany of Crete (Origanum Dictamnus), and a few other plants. It is often more difficult to distinguish bracts from the sepals of a polyphyllous calyx than

even from the leaves of the stem. In fact, there is in many cases no other mode than ascertaining the usual number of sepals in other plants of the same natural order, and considering every leaf-like appendage on the outside of the usual number of sepals as a bract. In Camellia, for example, if it were not known that the normal number of sepals of kindred genera is five, it would be impossible to determine the number of its sepals. When the bracts are very small, they are called *bractlets* (*bracteolæ*); or, if they are of different sizes upon the same inflorescence, the smallest receive that name. It rarely occurs that an inflorescence is destitute of bracts. In Crucifers this is a general character, and is observed by Link to indicate an extremely irregular structure. When bracts do not immediately support a flower or its stalk, they are called *empty* (*vacuæ*). As a general rule, it is to be understood, that whatever intervenes between the true leaves and the calyx, whatever be their form, colour, size, or other peculiarity, comes within the meaning of the term.

Under particular circumstances bracts have received the following peculiar names:—

When they are empty, and terminate the inflorescence, they form a *coma*, as in Green and purple Clary (Salvia Horminum), and in the common Pine Apple or Ananas. In such cases they are often enlarged and coloured.

If they are verticillate, and surround several flowers, they constitute an *involucre*. In Umbelliferous plants, the bracts which surround the general umbel are called an *universal involucre*; and those which surround the umbellules a *partial involucre*, or *involucel*.

In Composites, the involucre often consists of several rows of imbricated bracts, and has received a variety of names, for none of which there appears to be occasion. Linnæus called it *calyx communis*, Necker *perigynandra communis*, Richard *periphoranthium*, Cassini *periclinium*. There is often found at the base of the involucre of Composites an exterior rank of bracts, which Linnæus called *calyculus*; and such involucres as were so circumstanced *calyx calyculatus*. Cassini restricted the term *involucre* to this; but it seems most convenient to

call these exterior bracts *bractlets,* and to say that an involucre in which they are present is *basi bracteolatum,* bracteolate at the base.

Another form of the involucre is the *cupule* (*fig.* 66.) It consists of bracts not much developed till after flowering, when they cohere by their bases, and form a kind of cup. In the Oak the cupule is woody, entire, and scaly, with indurated bracts: in the Beech it forms a sort of coriaceous, valvular, spurious pericarp: in the Hazel Nut (*fig.* 65.) it is foliaceous and lacerated.*

In Euphorbia the involucre is composed of two whorls of bracts, consolidated into a cup, and assumes altogether the appearance of a calyx, for which it was for a long time mistaken.

The name *squamæ* or *scales* is usually applied to the bracts of the catkin; it is also occasionally used to indicate any kind of bract which has a scaly appearance.

The bracts which are stationed upon the receptacle of Composites, between the florets, have generally a membranous texture and no colour, and are called *paleæ,* Englished by some botanists *chaff of the receptacle.* The French call this sort of bract *paillette,* Cassini *squamelles.*

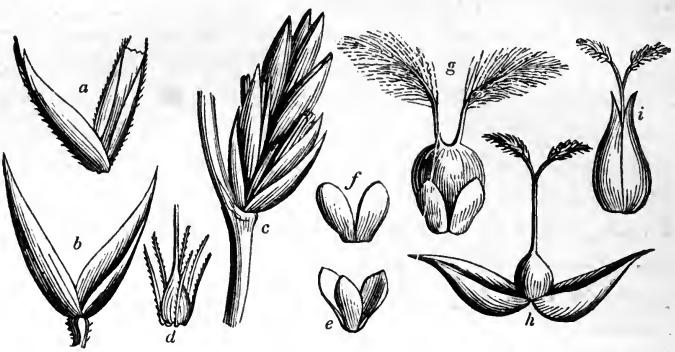
In Palms and Arads there is seated at the base of the spadix, a large coloured bract, in which the spadix, during æstivation, is wholly enwrapped, and which may, perhaps, perform in those plants the office of corolla. This is called the *spathe* (*fig.* 83.) Link considers it a modification of the petiole. (*Elementa,* p. 253.)

The most remarkable arrangement of bracts takes place in Grasses, in which they occupy the place of calyx and corolla, and have received a variety of names from different systematic writers. In order to explain the application of these terms, it is necessary to describe with some minuteness the structure of a *locusta* or *spikelet,* as the partial inflorescence of Grasses is denominated. Take, for example, any common Bromus; each spikelet will be seen to have at its base two opposite empty bracts (*fig.* 67. *b*), one of which is attached to

* What has been called the cupule of the Yew is said by Schleiden to be a late development of the primine of the ovule.

the rachis a little above the base of the other: these are the *glumes* of Linnæus and most botanists, the *gluma exterior* or

fig. 67.



calycinalis of some writers, the *tegmen* of Palisot de Beauvois, the *lepicena* of Richard, the *cætonium* of Trinius, and, finally, the *peristachyum* of Panzer. Above the glumes are several florets sitting in denticulations of the rachis (*fig.* 67. *c*): each of these consists of one bract, with the midrib quitting the blade a little below the apex, and elongated into a bristle called the *awn, beard,* or *arista,* and of another bract facing the first, with its back to the rachis, bifid at the apex, with no dorsal vein, but with its edges inflexed, and a rib on each side at the line of inflexion (*fig.* 67. *a*). These bracts are the *corolla* of Linnæus, the *calyx* of Jussieu, the *perianthium* of Brown, the *gluma interior* or *corollina* and *perigonium* of some, the *stragulum* of Palisot de Beauvois, the *gluma* of Richard, the *bâle* or *glumella* of De Candolle and Desvaux, the *paleæ* of others. When the *arista* proceeds from the very apex of the bracts, and not from below it, it is denominated in the writings of Palisot a *seta.* Within the last-mentioned bracts, and opposite to them, are situated two extremely minute, colourless fleshy scales (*fig.* 67. *e*), which are sometimes connate: these are named *corolla* by Micheli and Dumortier, *nectarium* by Linnæus, *squamulæ* by Jussieu and Brown, *glumellæ* by Richard, *glumellulæ* by Desvaux and De Candolle, *lodiculæ* by Palisot de Beauvois, and *periphyllia* by Link. Amidst these conflicting terms it is not easy to

determine which to adopt. I recommend the exterior empty bracts to be called *glumes;* those immediately surrounding the fertilising organs *paleæ* or *pales*; and the minute hypogynous ones *scales* or *squamulæ*.

The pieces of which these three classes of bracts are composed are called *valves* or *valvulæ* by the greater part of botanists; but, as that term has been thought not to convey an accurate idea of their nature, Desvaux has proposed to substitute that of *spathellæ*, which is adopted by De Candolle. Palisot proposed to restrict the term *glume* to the pieces of the glume, and to call the pieces of the perianthium *paleæ*. Richard called the pieces of both glume and perianthium *paleæ*, and the scales *paleolæ*. It seems to me most convenient to use the term *valvula*, because it is more familiar to botanists than any other, and because I do not see the force of the objection which is taken to it.

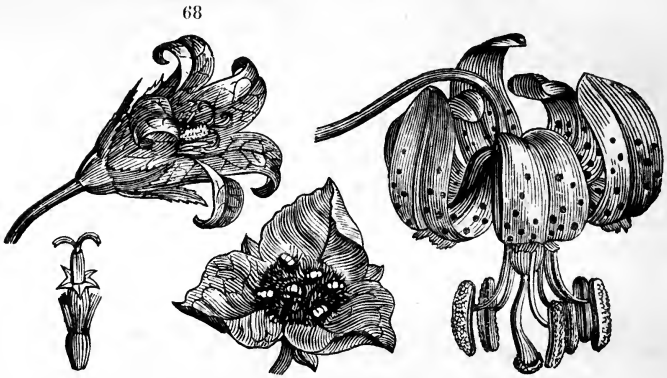
In the genus Carex two bracts (*fig.* 67. *i*, *h*) become confluent at the edges, and enclose the pistil, leaving a passage for the stigmas at their apex. They thus form a single urceolate body, named *urceolus* or *perigynium*. De Candolle justly observes, in his *Théorie*, that some botanists call this *nectarium*, although it does not produce honey; others *capsula*, although it has nothing to do with the fruit; but he does not seem to me more correct than those he criticises in arranging the urceolus among his miscellaneous appendages of the floral organs, which are "ni organes génitaux ni tégumens." I believe I was the first who explained the true nature of the urceolus, in my translation of Richard's *Analyse du Fruit*, printed in 1819 (p. 13.).

At the base of the ovary of some Sedges (Cyperaceæ) are often found little filiform appendages, called *hypogynous setæ* (*fig.* 67. *d*) by most botanists, and *perigynium* by Nees von Esenbeck. These are probably of the nature of the hypogynous scales of Grasses, and have been named *perispores* by some French writers.

Bracts are generally distinct from each other, and imbricated or alternate. Nevertheless, there are some striking exceptions to this; as remarkable instances of which may be cited Althæa and Lavatera among Mallowworts (Malvaceæ),

Euphorbia, all Teazelworts (Dipsacaceæ), many Composites, and some Trefoils, particularly my Trifolium cyathiferum, in all which the bracts are accurately verticillate, and their margins confluent, as in a true calyx.

4. Of the Flower.



"For a long time," says Schykoffsky, "a false opinion prevailed amongst Botanists, that the whole flower was but one organ, and even now that according to the latest theories the flower contains many organs more or less symmetrically arranged, they consider the place from whence proceed the sepals, the petals, the stamens, and the pistils, as a terminal nodus, whereas, by the undisputed affinity with bulbs, whether tunicate or squamate, it is impossible not to admit the existence at the place in question of several very short internodia. Agardh himself, considering the fruit as a terminal bud, consisting in its simplest form of one carpellary leaf, with the seed-bearing stalk in its axilla, does not by this view embrace the greater portion of the phenomena. According to my observations in many compound fruits, whether unilocular or plurilocular, with a so-called central or columnar placenta, there does not arise a separate bud from the axilla of each carpellary leaf, but the whole central support, or common seed-stalk, is the immediate prolongation of the floral axis or peduncle, forming an internodium above

the nodus, from whence proceed the carpellary leaves. It is then either covered with seeds, dispersed without any perceptible order, as in Primworts (Primulaceæ) and Cloveworts (Caryophyllaceæ), or it forms at a greater or less height a special nodus, from whence one or two seeds descend into each cell of the fruit, supported on distinct seminal pedicels, as in Mallowworts (Malvaceæ) with monospermous carpels, Phytolacca decandra, and all Spurgeworts (Euphorbiaceæ). In the latter family the seed-stem is already almost free, that is, the margins of the carpellary leaves scarcely adhere to it, and readily separate when ripe, without any laceration of the tissue."

The Flower is in fact a terminal bud enclosing the organs of reproduction by seed. By the ancients the term flower was restricted to what is now called the corolla; but Linnæus wisely extended its application to the union of all the organs which contribute to the process of fecundation. The flower, therefore, as now understood, comprehends the *calyx*, the *corolla*, the *stamens*, and the *pistil*, of which the two last only are indispensable. The calyx and corolla may be wanting, and a flower will nevertheless exist; but, if neither stamens nor pistil nor their rudiments are to be found, no assemblage of leaves, whatever may be their form or colour, or how much soever they may resemble the calyx and corolla, can constitute a flower.

We usually consider the flower to consist of a certain number of whorls, or of parts originating round a common centre from the same plane. But Adolphe Brongniart has correctly pointed out the fact that what we call whorls in a flower are in many cases not so, strictly speaking, but only a series of parts in close approximation, and at different heights upon the short branch that forms the axis. This is particularly obvious in a Cistus, where, of the five sepals, two are lower and exterior, and three higher and within the first. The manner also in which the petals overlap each other evidently points to a similar cause, although the fact of those pieces being inserted at different heights may not be apparent. (See *Annales des Sciences*, xxiii. 226.)

The flower, when in the state of a bud, is called the *alabastrus* (*bouton* of the French); a name used by Pliny for the rose-bud. Some writers say *alabastrum*, forgetting, as it would seem, that that term was used by the Romans for a scent-box, and not for the bud of a flower. Link calls the parts of a flower generally, whether united or connate, *moria*, whence a flower is *bi-polymorious* (*Elem.*, 243.); but I know of no other writer who employs these terms, which indeed are superfluous. It is more usual to introduce the Greek noun μερος, a part of anything, in connection with some numeral, as *pentamerous*, if a flower consists of organs in fives, *tetramerous*, if in fours, and so on. The same fact is indicated briefly by the signs $\sqrt[5]{}$ $\sqrt[4]{}$, &c.

The flowers of a capitulum, small, and somewhat different in structure from ordinary flowers, are called *florets* (*flosculi*; *elytriculi* of Necker; *fleurons* of the French.)

The period when a flower opens is called its expansion or *anthesis*; the manner in which its parts are arranged, with respect to each other, before the opening, is called the *æstivation*.

The expansion of a flower is either *centrifugal*, or *centripetal*—centrifugal when the central or uppermost flowers expand first—centripetal when the marginal or lowermost flowers expand first.

Æstivation is the same to a flower-bud as vernation is to a leaf-bud: the terms expressive of its modifications are to be sought in Glossology. This term æstivation is applied separately to the parts of which a flower may consist; thus, we speak of the æstivation of the calyx, of the corolla, of the stamens, and of the pistil; but not of the æstivation of a flower collectively.

5. Of the Inflorescence.

Inflorescence is a term contrived to express generally the arrangement of flowers upon a branch or stem. The part which immediately bears the flowers is called the *pedunculus* or peduncle, and is to be distinguished from any portion of a

branch by not producing perfect leaves; those which are found upon it, called *bracts,* being much reduced in size and figure from what are borne by the rest of the plant.

The normal position of the inflorescence is axillary to a leaf, the necessary consequence of its being a kind of branching. But in some plants, especially of the natural order of Nightshades (Solanaceæ) it grows apparently opposite the leaves. It is believed by some botanists that cases of such irregularity are caused by the peduncle, which is axillary to a leaf, contracting an adhesion with the internode above it, and not separating till it is opposite the succeeding leaf; but this is not supported by conclusive evidence. Flowers of this kind are called *oppositifolii.*

The term *peduncle,* although it may be understood to apply to all the parts of the inflorescence which bear the flowers, is practically only made use of to denote the immediate support of a single solitary flower, or of the whole mass of inflorescence, and is therefore confined to that part of the inflorescence which first proceeds from the stem. If it is divided, its principal divisions are called branches; and its ultimate ramifications, which bear the flowers, are named *pedicels.* There are also other names which are applied to its modifications. In plants which are destitute of stem, it often rises above the ground, supporting the flowers on its apex, as in the Cowslip; such a peduncle is named a *scape* (*hampe,* Fr.) Some botanists uselessly distinguish from the scape the *pedunculus radicalis,* confining the former term to the peduncle which arises from the central bud of the plant, as in the Hyacinth; and applying the latter to a peduncle proceeding from a lateral bud, as in Plantago media. When a peduncle proceeds in a nearly right line from the base to the apex of the inflorescence, it is called the *rachis,* or the *axis* of the inflorescence. This latter term was used by Palisot de Beauvois to express the rachis of Grasses, and is perhaps the better term of the two, especially as the term rachis is applied by Willdenow and others to the petiole and midrib of Ferns. In the spikelets of Grasses the rachis has an unusual, toothed, flexuose appearance, and has received the name of *scobina* from Dumortier; if it is reduced to a mere bristle, as

in some of the single-flowered spikelets, the same writer then distinguishes it by the name of *acicula*.

When the part which bears the flowers is repressed in its development, so that, instead of being lengthened into a rachis, it forms a flattened area on which the flowers are arranged, it becomes what is called a *receptacle;* or, in the language of some botanists, the *receptacle of the flower* (*fig.* 72.)

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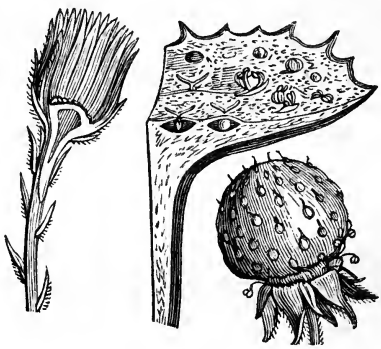

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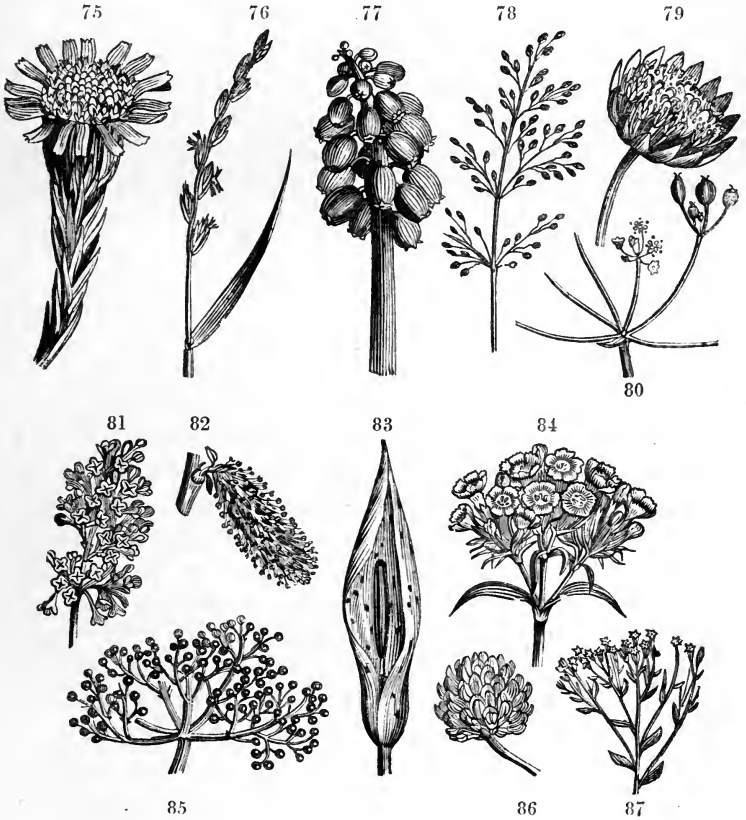
When the receptacle is not fleshy, but is surrounded by an involucre, it has been called the *clinanthium* (the *thalamus* of Tournefort,) as in Composites, or, in the language of Richard, *phoranthium:* Lessing calls this part the *rachis.* But if the receptacle is fleshy, and is not enclosed within an involucrum, as in Dorstenia (*fig.* 73.) and Ficus, it is then called by Link *hypanthodium;* the same writer formerly named it *amphanthium,* a term now abandoned. With receptacles of this sort, which are depressed and distended branches, are not unfrequently confounded parts of a different nature, as in the Strawberry, the soft, succulent centre of which (*fig.* 74.) is evidently the growing point, excessively enlarged, and bearing the carpels upon its surface. See RECEPTACLE at a future page.

According to the different modes in which the inflorescence is arranged, it has received different names, the right appli-

cation of which is of the first importance in descriptive botany. If flowers are sessile along a common axis, as in Plantago, the inflorescence is called a *spike* (*fig.* 76.); if they are pedicellate, under the same circumstances, they form a *raceme,* (*fig.* 77.), as in the Hyacinth: the raceme and the spike differ, therefore, in nothing, except that the flowers of the latter are sessile, of the former pedicellate. These are the true characters of the raceme and spike, which have been confused and misunderstood.



When the flowers of a spike are destitute of calyx and corolla, the place of which is taken by bracts, and when with such a formation the whole inflorescence falls off in a single

piece, either after flowering or ripening the fruit, as in the Hazel, Willow, Poplar, &c., such an inflorescence is called an *amentum* or *catkin* (*Catulus, Iulus, nucamentum,* of old writers, *fig.* 82.)

If a spike consists of flowers destitute of calyx and corolla, the place of which is occupied by bracts, supported by other bracts which enclose no flowers, and when with such a formation the rachis, which is flexuose and toothed, does not fall off with the flowers, as in Grasses, each part of the inflorescence so arranged is called a *spikelet* or *locusta.*

When the flowers are closely arranged around a fleshy rachis, which is enclosed in the kind of bract called a spathe (see p. 311.), the inflorescence is termed a *spadix* (*fig.* 83.) This is chiefly found in the Aral and Palmal alliances. It is frequently terminated, as at *fig.* 83., by a soft club-shaped mass of cellular substance which extends far beyond the flowers, and is itself entirely naked; this is an instance of a growing point analogous to what forms the spine of a branch, except that it is soft and blunt, instead of being hard and sharp-pointed.

The raceme has been said to differ from the spike only in its flowers being pedicellate: to this must be added, that the pedicels are all of nearly equal length; but in many plants, as the Candytuft (Iberis), the lower pedicels are so long that their flowers are elevated to the same level as that of the uppermost flowers; a *corymb* is then formed. This term is frequently used in an adjective sense, to express a similar arrangement of the branches of a plant or of any other kind of inflorescence: thus, in Stevia, the branches are said to be *corymbose;* in others, the panicle is said to be corymbose (*fig.* 87.); and so on. When corymbose branches are very loose and irregular, they have given rise to the term *muscarium;* a name formerly used by Tournefort, but not now employed.

If the expansion of an apparent corymb is centrifugal, instead of centripetal; that is to say, commences at the centre, and not at the circumference, as in Dianthus Carthusianorum, we then have the *fascicle* (*fig.* 84.); a term which may not incorrectly be understood as synonymous with

compound corymb. The modern *corymb* must not be confounded with that of Pliny, which was analogous to our *capitulum.*

When the pedicels all proceed from a single point, as in Astrantia, and are of equal length, or corymbose, we have an *umbel* (*fig.* 80.). If each of the pedicels bears a single flower, as in Eryngium, the umbel is said to be *simple* (*fig.* 79. *a*); but if they divide and bear other umbels, as in Heracleum, the umbel is called *compound;* and then the assemblage of umbels is called the *universal umbel,* while each of the secondary umbels, or the umbellules, is named a *partial umbel.* The peduncles which support the partial umbels are named *radii.* Louis Claude Richard confined the word umbel to the compound form, and named the simple umbel *sertulum;* but this was an unnecessary change.

Suppose the flowers of a simple umbel to be deprived of their pedicels, and to be seated on a receptacle or enlarged axis, and we have a *capitulum* or flower-head. If this is surrounded by an involucre, the compound flower, as it is inaccurately called by the school of Linnæus, of Composites, is produced; which is sometimes named by modern botanists *anthodium;* it is also called *cephalanthium* by Richard, *calathis* by Mirbel, *calathium* by Nees von Esenbeck. The flowers or florets borne by the flower-head in its circumference are usually flat or ligulate, and different from those produced within the circumference. Those in the former station are called *florets of the ray;* and those in the latter, *florets of the disk.*

If all the flowers are hermaphrodite in the flower-head, it is *homogamous;* if the outer are neuter, or female, and the inner hermaphrodite, or male, it is *heterogamous:* if on the same plant some flower-heads are composed entirely of male flowers, and others entirely of female flowers, such a plant is termed by De Candolle *heterocephalous.*

The *glomerule* or *glomus* is the same to a flower-head as the compound is to the simple umbel; that is to say, it is a cluster of flower-heads inclosed in a common involucre, as in Echinops.

All the forms of inflorescence which have been as yet

mentioned are to be considered as reductions of the spike or raceme. Those which are now to be described are decompositions, more or less irregular, of the raceme.

The first of these is the *panicle* and its varieties. The *simple panicle* differs from the raceme in bearing branches of flowers where the raceme bears single flowers, as in Poa (*fig.* 78.); but it often happens that the rachis itself separates into irregular branches, so that it ceases to exist as an axis, as in some Oncidiums; this is called by Willdenow a *deliquescent panicle*. When the panicle was very loose and diffuse, the older botanists named it a *juba;* but this is obsolete. If the lower branches of a panicle are shorter than those of the middle, and the panicle itself is very compact, as in Syringa, it then receives the name of *thyrsus*.

Suppose the branches of a deliquescent panicle to become short and corymbose, with a centrifugal expansion indicated by the presence of a solitary flower seated in the axils of the dichotomous ramifications, and a conception is formed of what is called a *cyme*. This kind of inflorescence is found in Sambucus, Viburnum, and other plants (*fig.* 85.).

If the cyme is reduced to a very few flowers, such a disposition has been called a *verticillaster* by Hoffmansegg. (*Verzeichniss z. Pflanz. Cult.*, ii. 203.) It constitutes the normal form of inflorescence in Labiates, in which two verticillasters are situated opposite each other in the axils of opposite leaves. By Linnæus, the union of two such verticillasters was called a *verticillus* or whorl; and by others, with more accuracy, a *verticillus spurius* or false whorl. Link terms this inflorescence a *thyrsula;* but Hoffmansegg's name seems preferable.

The following tabular view of the differences among inflorescences will probably tend to render the above remarks more clear:—

Flowers not placed on stalks,
- arranged upon a lengthened axis,
  - which is permanent, *Spike, Locusta, Spadix.*
  - which is deciduous, *Catkin.*
- arranged upon a depressed axis, *Capitulum, Glomerulus.*

Flowers placed on distinct stalks,
arranged upon a lengthened axis.
Stalks simple,
and of equal length, *Raceme.*
the lowermost the longest.
Inflorescence centripetal, *Corymb.*
——— centrifugal, *Fascicle.*
Stalks branched.
Inflorescence lengthened and centripetal. *Panicle.*
——— depressed and centrifugal, *Cyme, Verticillaster.*
arranged upon a depressed axis, *Umbel.*

It occasionally happens, as in the Vine, that the axis of some of the masses of inflorescence loses its flowers; but at the same time acquires the property of twining round any object within its reach, and so of supporting the stem, which is too feeble to support itself. Such axes form what is called a spurious tendril, or a *cirrhus pedunculari*s, and are a striking exception to the general rule that the tendril takes its rise from the petiole or midrib.

In the preceding account of the inflorescence I have treated the subject in a practical way, and with reference to the usage of Botanists. But the Messrs. Bravais, together with Schimper and Braun, and some others, led by their examination of the spiral arrangement of leaves into an investigation of the laws that regulate the arrangement of flowers, have proposed a new nomenclature and theory, of which the following is their own abstract (*Ann. Sc.*, N. S., viii. 28.) :—

1. The inflorescence is a union of flowers grouped together in mutual relation. It may often be divided into other groups, essentially homogeneous with respect to each other, and which we call *partial* inflorescences; these inflorescences may sometimes be themselves subdivided; but something arbitrary may be sometimes found in the manner of their decomposition.
2. The flowers, or partial inflorescences which perform the

part of them, have two distinct modes of evolution; the centripetal and the centrifugal.

3. The SPIKE is a centripetal inflorescence. (Plantago, Ribes, Leontodon, &c.). Any centripetal group whatever, such as a partial umbel, raceme, spike, capitulum, provided the peduncles are destitute of lateral bracts.
4. The COMPOUD SPIKE is centripetal, with two degrees of evolution; thus it is composed of partial inflorescences arranged centripetally, and these partial inflorescences are spikes. (Male flowers of Pinus.)
5. The CYME is a centrifugal inflorescence. (Hemerocallis flava, Tradescantia, Strelitzia, Lamium, Cornus, Syringa.) A centrifugal group, whose peduncles grow out of each other.
6. The THYRSE is an inflorescence at first centripetal afterwards centrifrugal. (Tamus, Delphinium, Laburnum.) A group of cymes disposed centripetally, as the flowers are in the spike.
7. The SARMENTIDIUM is an inflorescence of which the first evolution is centrifugal: its partial inflorescences may belong to either of the four previous forms. (Cichorium Intybus, Vitis, Geranium molle, Asclepias). A group of cymes or spikes arranged centrifugally, as the flowers are in the cyme.
8. The cyme of Monocotyledons appears to be typically *uninodal* *; it is *helicoid* †, or *scorpioid* ,‡ according as its peduncles are *homodromal* §, or *antidromal.* ‖ It may be *binodal* *, *trinodal* *, *multinodal* *, in its first ramifications; but it has a tendency to become uninodal in its ultimate ramifications.
9. The cyme of Dicotyledons is binodal, or multinodal; the second is sometimes a simple variety of the first. In the

* According as the peduncles bear 1, 2, or a variable number of nodes.

† Where the flowers are arranged in succession in a spiral around a *pseudothallus* (or axis of *uniparous*, that is one-peduncled, cymes, or sarmentidia, formed by a series of successive peduncles, fitted into each other in such a way that they seem to form but one and the same stalk, as in Hemerocallis fulva).

‡ Where the flowers are arranged in two rows parallel to the axis of the pseudothallus, as in Canna indica.

§ Where the direction of a spire is the same as on the central stem.

‖ Where the direction of a spire is the reverse of that on the central stem.

binodal cyme one of the nodes is homodromal, the other antidromal. These nodes have usually an unequal tendency to develope; if the homodromal node causes the abortion of its antagonist, the cyme becomes by degeneration helicoid, and scorpioid in the opposite case. The multinodal cyme offers no fixed rule in the spirals of its nodes; it generally finishes by degenerating into little binodal few-flowered or one-flowered cymes. We therefore may consider the binodal cyme as the type of the cymes of dicotyledonous plants.

10. The helicoid cyme has a straight pseudothallus, not excentrical, often vertical.
11. The scorpioid cyme has its pseudothallus rolled in a plane, excentrical, often horizontal volute, the two rows of flowers regarding the sky.
12. A cyme may be either axillary or terminal. By decomposing the last into partial axillary cymes, we often arrive at the discovery upon the latter of the laws which the entire cyme did not offer.
13. The multinodal cyme, with axillary cymes, and subject to this decomposition, is sometimes rather difficult to distinguish from the thyrse. If the axillary cymes are one-flowered, there may be a difficulty in distinguishing them from the spike.
14. Cymes have another method of centrifugal evolution by the development of accessory peduncles; these peduncles are of the same order as those which are born upon other nodes of the central peduncle, and are almost always antidromal.
15. Sarmentidia follow in their organisation the same laws as the cyme.

In this memoir of the Messrs. Bravais there is much which is ingenious; but their system is founded upon theoretical refinements, which require much simplification, before they can be advantageously applied to practical purposes and it can hardly be regarded of such value as to be entitled to supersede the existing well-known nomenclature of the Inflorescence.

6. Of the Calyx.

The *calyx* is the external integument of the Flower, consisting of several verticillate leaves, either united by their margins or distinct, usually of a green colour, and of a ruder and less delicate texture than the corolla.

Authors have long disputed about the definition of a calyx, and the limits which really exist between it and the corolla: the above, which is copied from Link, seems to be the only one that can be considered accurate. In reality in many cases they pass so insensibly into each other, as in Calycanthus and Nymphæa, that no one can say where the calyx ends and the corolla begins, although it is evident that both are present. Linnæus, indeed, thought that it was possible to distinguish them by their position with regard to the stamens, asserting that the divisions of the calyx are opposite those organs, and of the corolla alternate with them; but, if this distinction were admitted, the corolla of the Primrose would be an inner calyx, which is manifestly an absurdity. Jussieu defines a calyx by its being continuous with the peduncle, which the corolla never is; and this may seem in some cases a good distinction: but there are plenty of true calyxes, of all Papaveraceous and Cruciferous plants, for instance, in which the calyx is deciduous, and not more continuous with the peduncle than the corolla itself. The only just mode of distinguishing the calyx seems to me to be to consider it in all cases the external verticillate series of the integuments of the flower within the bracts, whether it be half-coloured deciduous, and of many pieces, as in Crucifers; membranous and wholly-coloured, as in Mirabilis; green and campanulate, or tubular, as in Laurus and Lythrum. Upon this principle, whenever there is only one series of floral integuments, that series is the calyx. A calyx, therefore, can exist without a corolla; but a corolla cannot exist without a calyx, either perfect or rudimentary.

The term Perianth is sometimes given as synonymous with calyx; but this is an error.

The word Perianth signifies the calyx and corolla com-

bined, and is therefore strictly a collective term. It should only be employed to designate a calyx and corolla, the limits of which are undefined, so that they cannot be satisfactorily distinguished from each other, as in most Monocotyledonous plants, the Tulip and the Orchis for example. But since, even in such plants as these, there can be no reasonable doubt that the three outer floral leaves are the calyx, and the three inner the corolla (as is shown both by Tradescantia and its allies, in which the usual limits between calyx and corolla exist, and also by the usual origin of those parts in two distinct whorls), the utility of the term Perianth is rendered extremely confined. It is often a mere evasion of the task of ascertaining the exact nature of the floral envelopes in doubtful cases. Some writers, among whom are Link and De Candolle, have substituted *Perigonium* for Perianthium: but the latter is in most common use, its application is well understood, and there is no good reason for its being changed. Ehrhart, with whom the name Perigonium originated, called it double when the calyx and corolla are evidently distinct, and single if they are not distinguishable: but this use of terms is obsolete.

The divisions of a calyx are called its *sepals* (*sepala*); a term first invented by Necker, and revived by De Candolle. Botanists of the school of Linnæus call them the leaflets or foliola. Link says the word sepalum is barbarous, and proposes to substitute *phyllum*. The sepals are generally longer than the corolla in æstivation, and during that period act as its protectors: during flowering they are mostly shorter.

The calyx, in ordinary cases, if deciduous, falls off from the peduncle by its base. In many cases the sepals drop off separately, as leaves fall from the stem; but occasionally they cohere firmly into a sort of cap or lid, which is pushed off entire by the increase of the corolla and stamens: in these cases the calyx is said to be *operculate*, if it falls off without any lateral rupture of its cap, as in Eucalyptus; and *calyptrate*, if at the period of falling it bursts on one side, as in Eschscholtzia. In the former of these two cases, the cohesion between the sepals is complete and never destroyed; in the

latter, two of the sepals separate, the cohesion between the remainder continuing complete.

The calyx of Composites is so very different in appearance from the calyx of other plants, that it is known by the particular name of *pappus*. It usually consists of hair-like processes proceeding from the apex of the ovary, in which case it is said to be *pilose:* if those hairs are themselves divided, it is *plumose;* if they are very unusually stiff, it is *setose,* in which case the setæ are often reduced in number to two, or even one; if the divisions of the pappus are broad and membranous, it is said to be *paleaceous:* finally, it is sometimes reduced to a mere rim: in which case it is said either to be *marginate,* or to be *none*—to have no existence. A calyx appears to be brought into this state by having no room to develope, in consequence of the pressure of the surrounding flowers. In such cases as this, where the calyx is altogether obsolete, the definition of that organ, as the most external of the floral envelopes, appears to be destroyed: but there can be no doubt that it is present in the form of a membrane adhering to the side of the ovary, although it is not visible to our eyes. The same may be said of such plants as those Acanthads (*Vegetable Kingdom,* p. 678), in which, although the calyx is reduced to a mere ring, yet it does exist in the shape of that ring.

The Calyx being composed of leaves analogous to those of the stem, but reduced in size and altered in appearance, it will follow that it is subject to the same laws of development as stem-leaves; and, as the latter, in all cases, originate immediately from the axis, *below* those that succeed them in the order of development, so the calyx must always have an origin beneath those other organs which succeed it in the form of corolla, stamen, and pistil or ovary. Hence has arisen the axiom in botany, that whatever the apparent station of the calyx may be, it always derives its origin from below the ovary: nevertheless, it is often said to be superior.

If it is distinct from the ovary, as in Silene, it is said to be *inferior* or *free* (*calyx inferus,* or *liberus*); and the ovary is then called *superior* (*ovarium superum,* or *liberum*) (Plate V. fig. 3.); but if it is firmly attached to the sides of the ovary,

so that it cannot be separated, as in Myriophyllum, it is then called *superior*, or *adherent* (*calyx superus*, or *adhærens*), and the ovary *inferior* (*ovarium inferum*) (Plate V. fig. 7. 9.). From what has been said of pappus it will be obvious that it is a *superior calyx*.

The general opinion of botanists, in regard to the real nature of the superior calyx, is such as I have stated; and the accuracy of it in the majority of cases is indisputable: but it is by no means certain that, in some instances, what is called the tube of the calyx is not, as I have long since stated (*Introduction to the Natural System*, p. 26.), "sometimes a peculiar extension or hollowing out of the apex of the pedicel, of which we see an example in Eschscholtzia, and of which Rosa and Calycanthus, and, perhaps, all supposed tubes without apparent veins, may also be instances." And if this be so, the calyx may be superior in consequence of the cohesion of the ovary with the inside of an excavated pedicel, and not with the calyx itself.

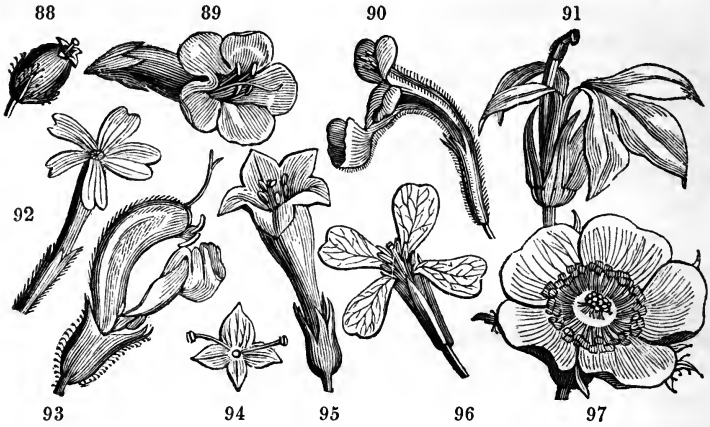
When the sepals cohere by their contiguous edges into a kind of tube or cup, the calyx is said to be *monophyllous* or *monosepalous*; an inaccurate term, which originated when the real nature of organs was unknown, and when a monophyllous calyx was thought to consist really of a single leaf, clipped into teeth at its margin. To avoid this inaccuracy, the word *gamosepalous* has been proposed, but it is not much employed; and in truth the term *monos* may be taken to signify either *one* or *united into one*, the latter of which is correct. That the sepals are originally all distinct is not a matter of theory, but, as Schleiden rightly observes, of investigation established by actual evidence.

Various terms are employed to express the degree in which the sepals of a monosepalous calyx cohere: they will be explained in Glossology. When no cohesion whatever takes place between the leaves of a calyx, the term *sepalous* is employed with that Greek numeral prefixed, which is equivalent to the number of pieces; as, for example, if they are two, the calyx is disepalous; if three, trisepalous; if four, tetrasepalous, and so on.

Sometimes the calyx has certain expansions or dilatations,

as in Scutellaria and Salsola. These are generally named *appendages*, and such a calyx is said to be *appendiculate*; but Mœnch has proposed a particular term for them, *peraphyllum*, which is, however, never used.

7. Of the Corolla.



That envelope of the flower which forms a second whorl within the calyx, and between it and the stamens, is called the *corolla*. Its divisions always, without exception, alternate with those of the calyx, and are called *petals*. Like the sepals, they are either united by their margins, or distinct; but, unlike the calyx, they are rarely green, being for the most part either white, or of some colour, such as red, blue, or yellow, or of any of the hues produced by their intermixture. The corolla is generally also larger than the calyx.

Necker called the corolla *perigynandra interior*, and Linnæus occasionally gave it the name of *aulæum*, a term literally signifying the drapery of a room.

The alternation of the segments of the corolla with those of the calyx is a necessary consequence of their both being modifications of whorls of leaves, and therefore subject to the same laws of arrangement. If two whorls of leaves are examined, those of Galium, for example, they will always be

found to be mutually so arranged, that if the internode which separates them were removed, the leaves would exactly alternate with each other; and as there are no known exceptions to this law in real leaves, it is natural that it should not be departed from in any modifications of them.

Nevertheless, M. Dunal has imagined that when two organs are opposite each other in the same flower, they exhibit a case of what he calls unlining (*dédoublement*, or *deduplication*), assuming that in certain cases there is a tendency on the part of an organ to divide or separate into two or more layers, each having the same structure.

The manner in which M. Dunal and his followers speak of this imaginary quality is as follows:—

"De Candolle has observed, in his *Organographie Végétale*, that the multiplication of the organs of a flower belongs to two different systems: 1st, the increase of the number of whorls by other whorls similar to one of them; 2nd, by the increase of the number of pieces of one and the same whorl by the occasional development of organs similar to those of which the whorl is composed. The multiplications or unlinings which I have mentioned, belong to the last system, with this difference, that in the cases I have noticed they are not occasional or accidental, but habitual. I said, when speaking about them, 'All organs of plants, originally united, separate in different ways, in different proportions, and then appear under different aspects. They all pass out of each other (*désemboîtent*); they all unline; but they sometimes separate even when they are generally united in the plane of their general symmetry; or, which is the same thing, we find many organs where we ought to find but one single one . . . . . When, for example, we find several stamens instead of one normal one, I say that they are produced by the unlining or multiplication of the primitive stamen, &c.

"This phenomenon being well understood, let us examine the expressions employed to signify it. That of multiplication is tolerably correct, but very vague. The term unlining is more precise; it is a better explanation of the fact, as I understand it; that is to say, a separation of parts originally closely united, since they spring from one single fibre. This

separation is frequently observed in the fibres of stems; but to confine my attention to flowers, I shall just notice that the single fibre which forms the base of certain stamens, produces three stamens at its top in Monsonia, seven or more in Melaleuca, a greater number in Hypericum ægyptiacum, &c. In some plants these different degrees of separation are successive, so that they can be traced by the eye. In Malva abutiloides, for example, we find a great number of stamens developing one after the other on the outside of a cylindrical column. On looking at the base of the latter we find traces of five bundles opposite the petals. If a transverse section of this column is made a little above the ovary, we see the sections of two fibres opposite each petal. A little lower but one fibre is found; higher up, on the contrary, we find a great quantity. The same phenomenon is still more evident in another genus of the same natural order. From the hollow cylinder formed by the union of the base of the petals and stamens of Pachira marginata, instead of one single stamen we find that there rises one fibre or cylindrical body, which soon separates into two or three parts, each of which is again divided, and so on, until we come to those that carry the anthers. Here we have a succession of true unlinings; but in Crucifers, and especially in Sterigma and Anchonium, the large stamens offer an example of simple unlining in the full meaning of the word, since they present a separation into two parts only. I thought I might extend the primitive meaning of the word deduplication, and consider it as synonymous with separation, disjunction, in the same way as we speak of 'doubling the pace,' 'doubling a track,' to express an increase in velocity of any sort, &c. If, notwithstanding this explanation, anybody should object to the word I have employed, I propose *Chorisis* (χωρισις, separatio, disjunctio, divisio,) to define what I have called deduplication, and the adjective *choristate*, to signify unlined.

"But to return to our subject, we can say that in Peganium Harmala, there are two stamens opposite each petal by simple deduplication, or by binary chorisis of the normal stamen, or again, that there are two choristate stamens opposite each petal. All these expressions mean that instead of finding

stamens equal in number to the petals, and opposite to them one to one, we find several stamens opposite one and the same petal, and this in consequence of the separation of a determinate number of bundles arising from the fibre which should have produced one single normal stamen, a separation which often takes place before the point of exsertion of such choristate, unlined or multiplied stamens, according as each botanist may choose to call them." (*Considerations, &c.* p. 34).

But this hypothesis appears to me destitute of real foundation for the following reasons :—

1. There is no instance of unlining which may not be as well explained by the theory of alternation.

2. It is highly improbable and inconsistent with the simplicity of Vegetable Structure, that in the same flower the multiplication of organs should arise from two wholly different causes; viz., alternation at one time and unlining at another.

3. As it is known that in some flowers, where the law of alternation usually obtains, the organs are occasionally placed opposite each other, it is necessary for the supporters of the unlining theory to assume that in such a flower a part of the organs must be alternate and a part unlined, or at one time be all alternate and at another time be all unlined, which is entirely opposed to probability and sound philosophy. (See the Camellias figured in the *Elements of Botany*, p. 76., figs. 156, 157, 158.)

4. The examination of the gradual development of flowers, the only irrefragable proof of the real nature of final structure, does not in any degree show that the supposed process of unlining has a real existence.

Nevertheless, the theory of deduplication has its supporters among French Botanists of eminence.

When the petals of a corolla are all distinct, then the corolla is said to be *polypetalous;* but if they cohere at all by their contiguous margins, so as to form a tube, it then becomes what is called *monopetalous;* a term of the same origin as that of monophyllous, in regard to calyx (*see* p. 329), and for which that of *gamopetalous* has been sometimes substituted.

If the petals adhere to the bases of the stamens, so as to

form a sort of spurious monopetalous corolla, as in Malva and Camellia, such a corolla has been occasionally called *catapetalous;* but this term is never used, all such corollas being considered polypetalous.

When the petals are confluent into a monopetalous corolla, they constitute what is called a *tube;* the orifice of which is the *faux* or *throat.* The principal forms of such a corolla are rotate (*fig.* 94.), hypocrateriform (*fig.* 92.), infundibuliform (*fig.* 95.), campanulate (*fig.* 96.), and labiate (*fig.* 93.). When the divisions of a monopetalous corolla do not, as in Campanula, spread regularly round their centre, but part take a direction upwards, and the remainder a direction downwards, as in Labiates, the upper form what is called the *upper lip,* and the lower, the *lower lip,* or *labellum;* the latter term is chiefly applied to the lower lip of Orchidaceous plants. If the upper lip is arched, as in Lamium album, it is termed the *galea* or *helmet.* When the two lips are separated from each other by a wide regular orifice, as in Lamium, the corolla is said to be *labiate* or *ringent;* if the upper and lower sides of the orifice are pressed together, as in Antirrhinum, it is *personate* or *masked,* resembling the face of some grinning animal. In the latter the lower side of the orifice is elevated into two longitudinal ridges, divided by a depression corresponding to the sinus of the lip; this part of the orifice is called the *palate.* In ringent and personate corollas the orifice is sometimes named the *rictus;* but this term is superfluous and little used.

A petal consists of the following parts:—the *limb* or *lamina;* and the *unguis* or *claw.* The claw is the narrow part at the base which takes the place of the foot-stalk of a leaf, of which it is a modification; the limb is the dilated part supported upon the claw, and is a modification of the blade of a leaf. In many petals there is no claw, as in Rosa; in many it is very long, as in Dianthus. When the claw is present, the petal is said to be *unguiculate.* In some unnaturally deformed flowers the limb is absent, as in the garden variety of Rose, called R. Œillet, in which the petals consist wholly of claw.

According to the manner in which the petals of a polype-

talous corolla are arranged, they have received different names, which are thus defined by Link :—the *rosaceous* corolla (*fig.* 97.) has no claw, or it is very small; the *liliaceous* (*fig.* 71.) has its claws gradually dilating into a limb, and standing side by side; a *caryophyllaceous* has long, narrow, distant claws; the *alsinaceous* has short distant ones; the *cruciate* flower has four valvaceous sepals, four petals, and six stamens, of which two are shorter than the rest, and placed singly in front of the lateral sepals, and four longer, and standing in pairs opposite the two other sepals. If the corolla is very irregular, with one petal very large and helmet-shaped, or hooded, as in the calyx of Aconitum, it is sometimes called *cassideous;* if it resembles what is called labiate in monopetalous corollas, it is termed *labiose.* The corolla of the Pea, and most Leguminous plants, has received the fanciful name of *papilionaceous* or *butterfly-shaped,* (*figs.* 98, 99.); in this

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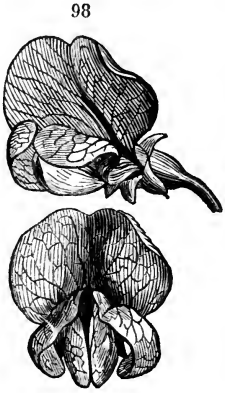

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there are five petals, of which the upper is erect and more expanded than the rest, and is named the *standard* or *vexillum;* the two lateral are oblong, at right angles with the standard, and parallel with each other, and are called the *wings* or *alæ;* and the two lower, shaped like the wings and parallel with them, cohere by their lower margin, and form the *keel* or *carina.* The wings were formerly called *talaræ* by Link, and the keel *scaphium* by the same author.

When the corolla is very small, or when it forms a part

of a capitulum, it is called *corollula:* that of a floret is so named.

If the flower has no corolla, it is said to be *apetalous.*

Sometimes a petal is lengthened at the base into a hollow tube, as in Orchis, &c.: this is called the spur or *calcar,* and by some *nectarotheca.*

In Umbelliferous plants the petal is abruptly acuminate; and the acumen is inflexed. The latter is named the *lacinula.*

A corolla is said to be *regular* when its segments form equal rays of a circle supposed to be described with the axis of the flower for a centre. If they are unequal, the corolla is called *irregular. Equal* and *unequal* are occasionally substituted for regular and irregular.

In anatomical structure, the petal should agree with a leaf, of which it is a mere modification; and, in fact, it does so in all that is important, its differences consisting chiefly in a diminished size, an attenuation and colouring of the tissue, with a suppression of the pleurenchym. Like a leaf, petals consist of a flat plate of parenchym, articulated with the stem, traversed by veins, and frequently having stomates upon its surface. Their veins consist almost entirely of delicate spiral vessels, upon which the parenchym is immediately placed. It is therefore by mistake that De Candolle has stated (*Organogr.,* p. 454.) that stomates and spiral vessels are usually absent. In some plants the petals remain after the flowering is over, and then grow into true leaves.

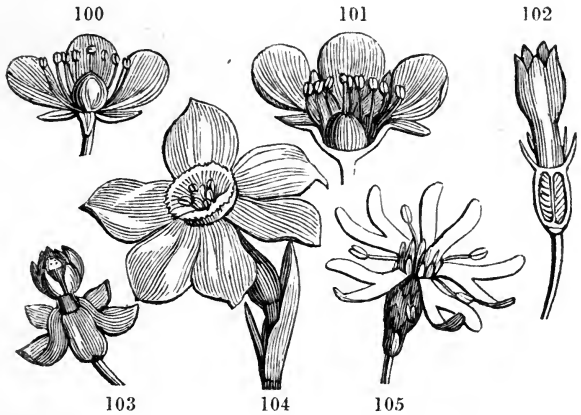
The petals are usually deciduous soon after flowering, or even at the instant of expansion; a very rare instance of their persistence and change from minute colourless bodies into leafy, richly coloured expansions, occurs in Melanorrhæa usitatissima.

Their colours are due to the secretion within the cells of their parenchym of a peculiar substance: even white petals are so in consequence of the deposit of an opaque white substance, and not because of the absence of colouring matter.

In most corollas the petals, in their natural state, form but one whorl within that of the calyx: but instances exist in which they naturally are found in several whorls, as in

Nymphæa, Nuphar, Magnolia, &c. It sometimes happens that, if there is more than one row of petals, all within the first row assume a different appearance from the first; the filamentous processes of the crown of Passiflora are apparently of this nature.

The petals are often furnished with little appendages (*fig.* 105.), which are either inner rows of petals in a state of adhesion to the first row, or modified stamens; which of the two it is sometimes difficult to ascertain. Many of these enter into Linnæus's notion of *nectarium*, although nearly the whole of them are destitute of any power of secreting *nectar* or honey.



The most common form of appendage is the *coronet* or *corona*, which proceeds from the base of the limb, forming sometimes an undivided cup, as in Narcissus (*fig.* 104.), when it becomes the *scyphus* of Haller; sometimes dividing into several foliaceous erect scales, as in Silene and Brodiæa, when it forms the *lamella* of some writers; occasionally appearing as cylindrical or clavate processes, as in Schwenckia and Tricoryne, where it is manifestly modified stamens; and even in some instances forming a thick solid mass covering over the ovarium, and adhering to the stamens, as in Stapelia, when it is called the *orbiculus*. Parts of this last form of coronet bear several names, which are found useful in avoiding repetition when describing the complicated structure of

this kind of appendage. The whole mass of the coronet is the *orbiculus*, or *saccus*, or *stylotegium*; certain horn-like processes are *cornua*, or horns; the upper end of these is the beak, or *rostrum*, and their back, if it is dilated and compressed, is the *ala*, or *appendix*; occasionally there is an additional set of horns proceeding from the base of the orbiculus, and alternate with the *horns*, these are *ligulæ*; the circular space in the middle of the top of the orbiculus is the *scutum*. Brown names the orbiculus *corona staminea*, and its divisions *foliola*, or leaflets.

In some plants as Cynoglossum, the lamellæ are very small, scale-like, and overarch the orifice of the tube; such have received the name of *fornices*.

Link calls every appendage which is referable to the corolla a *paracorolla*; or, if consisting of several pieces, *parapetalum*; and every appendage which is referable to the stamens a *parastemon*. The filiform rays of the coronet of Passiflora the same author calls *paraphyses* or *parastades*.

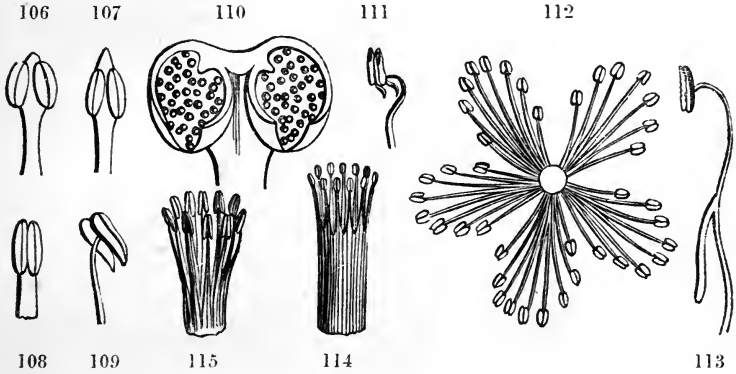
Mœnch names such appendages of the corolla as the filamentous beard of Menyanthes *perapetalum*, and Sprengel calls the same thing *nectarilyma*.

In Ranunculus there exists at the base of each petal a little shining, sometimes elevated, space which secretes honey. This is the true *nectarium* or *nectarostigma* of Sprengel. By some writers it has been considered a kind of reservoir, in which there is some plausibility; but it seems, from analogy, to be rather a barren stamen, united with the base of the petal, and of the same nature as the lamella of other plants.

8. Of the Stamens.

Next the petals, in the inside, are seated the organs called *Stamens*—the *Apices* of old botanists. These constitute the *Andrœceum* or male apparatus of the flower, like the calyx and corolla are modifications of leaves, and consist of the *filament*, the *anther*, and the *pollen*, of which the two latter are essential: the first is not essential; that is to say, a stamen may exist without a filament, but it cannot exist without an anther and pollen. All bodies, therefore, which resemble

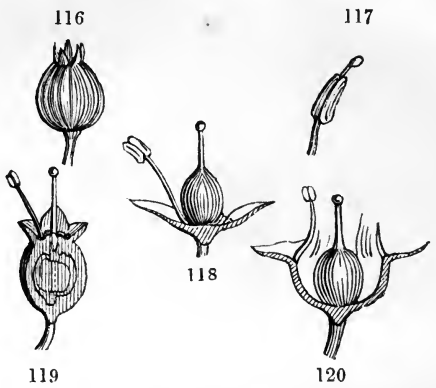
stamens, or which occupy their place, but which are destitute of anther, are either petals, or appendages of the petals, or abortive stamens.



As the petals are naturally alternate with the sepals, so the natural station of the stamens, if of equal number with the petals, is alternately with them; and all deviations from this law are to be understood as irregularities arising from the suppression or addition of parts. Thus, when in the Primrose we find the stamens opposite the segments of the corolla, and equal to them in number, it is to be supposed that those stamens which are present constitute the second of two rows of which the exterior is not developed; and when in Silene we find the stamens ten, while the petals are five, the former are to be considered to consist of two rows, although appearing to consist of one. This may be understood by examining Oxalis, in which the stamens are all apparently in one row, but are alternately of different lengths. When the number of stamens exceeds twice that of the petals, they will still be divisible by the number of which they were at first a multiple, until their number is excessively increased, when they seem to cease to bear any kind of proportion to the petals.

The stamens always originate from the space between the base of the petals and the base of the ovary. But botanists are nevertheless in the habit of saying that they are inserted into the calyx or corolla (*fig.* 120.) (*perigynous*), or under the pistil (*fig.* 118.) (*hypogynous*), or into the pistil (*fig.* 119) (*epigynous*),

all which expressions are inaccurate, and lead to erroneous notions of structure. The student, therefore, must understand, that when in the Primrose the stamens are said to be inserted into the mouth of the corolla, it is meant that they



cohere with the corolla as far as the mouth, where they first separate from it; when in the Rose they are said to be inserted into the calyx, it is meant that they cohere with the calyx up to a certain point, where they separate from it; when in Arabis they are said to be inserted under the pistil, it is meant that they cohere with neither calyx nor corolla, but stand erect from the point which immediately produces them; and finally, when in Orchis or Heracleum they are said to be inserted into the pistil, such an expression is to be taken as meaning that they cohere with the pistil more or less perfectly. For excellent arguments in support of this hypothesis, see Dunal's *Considérations sur la nature et les rapports de quelques uns des Organes de la Fleur*. I do not use them or any such, here, because it seems to be so self-evident a fact, when once pointed out, as to require no demonstration, and can easily be ascertained to be true by actual inspection of a flower in its different stages of growth. It is, however, to be recollected that in some cases the peduncle is supposed to be hollowed out (see page 329); and when that occurs the origin of the stamens will be theoretically at the orifice or edge of the supposed excavation.

When the filaments are combined into a single mass, the

mass is said to be a fraternity, brotherhood or *adelphia:* if there is one combination, as in Malva, they are *monadelphous* (*fig.* 114.); if two, as in Fumaria or Pisum, *diadelphous;* if three, as in some Hypericums, *triadelphous;* if several, as in Melaleuca, *polyadelphous* (*fig.* 112.). The tube formed by the union of the filaments in a monadelphous combination is called, by Mirbel, *androphorum.*

If the stamens are longer than the corolla they are *exserted;* if shorter, they are called *included:* when they all bend to one side, as in Amaryllis, they are *declinate;* if two out of four are shorter, they are *didynamous;* if four out of six are longest, they are *tetradynamous.*

The *number* of stamens is indicated by a Greek numeral prefixed to the word *androus,* which signifies male, thus:—

One stamen	is	Monandrous.
Two	—	Diandrous.
Three	—	Triandrous.
Four	—	Tetrandrous.
Five	—	Pentandrous.
Six	—	Hexandrous.
Seven	—	Heptandrous.
Eight	—	Octandrous.
Nine	—	Enneandrous.
Ten	—	Decandrous.
Eleven or twelve stamens,		Dodecandrous.
Twelve to twenty	—	Icosandrous.
Above twenty	—	Polyandrous or Indefinite.

The *filament* (Plate III.) (*capillamentum,* or *pediculus,* of some) is the part that supports the anther. It consists of a bundle of delicate woody tissue and spiral vessels, surrounded by cellular tissue, and is in all respects the same as the petiole of a leaf, of which it is a modification, except that its parts are more delicate. As the petiole is unessential to the leaf, so is the filament to the anther, it being frequently absent, or at least so strictly united to the sides of the calyx or corolla as to be undistinguishable. Its most common figure is filiform or cylindrical (Plate III. fig. 12, 13. 20, 21.), and it is almost

always destitute of colour; but there are exceptions to both these characters. In Fuchsia, for instance, the filaments are red like the petals; in Adamia they are blue; in Œnothera they are yellow; and a return to the foliaceous state of which they usually are a distinct modification is by no means rare. (Plate IV. fig. 6. 8.). Thus the filament in Canna is undistinguishable from petals except by its having an anther; in the same genus and its allies, and in all Gingerworts (Zingiberaceæ), the inner series of what seem to be petals are modifications of filaments (see *Vegetable Kingdom*, pp. 162, &c.): and this is a very common circumstance in sterile stamens.

A remarkable modification of the filament has been observed in Spironema fragrans. In that plant the epidermis of this organ is excessively thin, hardly adheres to the tissue below it, and incloses a bundle of spiral vessels too long for the sheath of skin, so that, while the latter is straight and even, the former are forced into a spiral direction for want of room to straighten.

The filament also varies in other respects: in Thalictrum it is thickest at the upper end, or *clavate* (Plate III. fig. 23.); in Mahernia *geniculate* (Plate III. fig. 25.), in Hertella *spiral*, in Crambe *bifurcate*, in Anthericum *bearded* or *stupose*. In some plants the filaments are combined into a solid body called the *columna*, as in Stapelia, Stylidium (Plate IV. fig. 1, 2, 3.), Rafflesia, and others: this has in Orchids received from Richard the name of *gynostemium*.

Care must be taken not to confound the pedicel and single stamen of the naked male flowers of Euphorbia with a filament, as was done by all writers, until Brown detected the error. For modifications of filaments see Plates III. and IV.

The Anther (*Theca* of Grew; *Capsula*, Malpighi; *Apex*, Ray; *Testiculus* or *Testis*, Vaillant; *Capitulum*, Jungius; *Spermatocystidium*, Hedwig) is a body generally attached to the apex of the filament, composed of two parallel lobes or cells (*thecæ*, or *coniothecæ*, or *loculi*,) containing *pollen*, and united by the *connective*. It consists entirely of cellular tissue, with the exception sometimes of a bundle of very minute

vascular tissue, which diverges on each side from the filament, and passes through that part of the anther from which the pollen has been incorrectly supposed to separate, and which is called the *receptacle* of the *pollen* by some, the *trophopollen* by Turpin, and the *raphe* by Link, but with greater propriety the *septum* of the anther. Its coat is called by Purkinje *exothecium*.

In the most common state of the anther the cells are parallel with each other (Plate III. fig. 14.), and open with two *valves* (Plate III. fig. 13. *a*), by a longitudinal fissure from the base to the apex; in Labiates and Figworts (Scrophulariaceæ) the cells diverge more or less at the base (Plate III. fig. 15. 18.), so as in some cases to assume the appearance of a one-celled horizontal anther, especially after they have burst. In Cucurbits the lobes are very long and narrow, sinuous, and folded back upon themselves (Plate III. fig. 24.). In Salvia the connective divides into two unequal portions, one of which supports a cell and the other is cell-less; in this case the connective has been called by Richard, *distractile*. Lacistema (Plate IV. fig. 7.) affords another instance of a divided connective. In many of the cases of excessive divergence of the cells the line of dehiscence of the anther is changed from longitudinal to vertical (Plate III. fig. 20. 17.), and has actually been supposed to be really transverse; an error which in most cases has arisen from not understanding the real structure of the anther. Some anthers, however, no doubt have cells that burst transversely, as Lemna, Alchemilla arvensis, Securinega, &c. (See Plate III. fig. 12. 16. 30.)

All anthers are not two-celled, their internal structure being subject to several modifications. It sometimes happens that the anther is four-celled, as in Tetratheca. In Epacris the two ordinary cells become confluent into one, and the anther is therefore one-celled. In Maranta and Canna only one cell is produced, the other being entirely suppressed. In most Amarants, Epacrids, and some other plants, the anther seems to be absolutely one-celled. (Plate IV. fig. 8.)

Of all these the four-celled anther is the type, and both the one-celled and two-celled are probably mere modifications

of it, depending upon whether the septa which originally exist all remain complete, or are half-absorbed, or wholly absorbed. Schleiden says he has found the anther before its bursting quadrilocular in more than one hundred families; amongst which may be named Grasses (Graminaceæ), Sedges (Cyperaceæ), Lilyworts (Liliaceæ), Labiates, Borageworts, Figworts (Scrophulariaceæ), Composites, Umbellifers, Crowfoots (Ranunculaceæ) with their allies, Roseworts, and Leguminous plants, which orders alone constitute almost one-half of the entire vegetation of the globe. It has been often asserted, he says, that the anther could not originally be quadrilocular, because it opens by two fissures only; which is as much as to consider two rooms in a house as one, because they have not folding doors, but single doors placed close together. Properly speaking, every anther really opens with four fissures; they appear, however, only as two, because each pair lies at the side of the common septum.

Other deviations from the normal form of anther occur, which are less easy to reconcile with the idea of a two-celled type. In some Laurels the anther is divided into four cells, one placed above the other in pairs; in Ægiceras it consists of numerous little cavities; and in the singular genus Rafflesia the interior is separated into many cellules of irregular figure and position, described by Brown as "somewhat concentrical, longitudinal, the exterior ones becoming connivent towards the apex, sometimes confluent, and occasionally interrupted by transverse partitions." In these instances the septa may be understood to arise from portions of the cellular tissue of the anther remaining unconverted into pollen.

According to Mr. Gardner, the anthers of Durio Zeylanicus are destitute of cells, the pollen grains being naked, and entirely surrounding a globose fleshy receptacle. Upon inquiring how far this might be owing to the age of the organ, he found that the same structure exists in the bud as in the expanded flower. Although this globular anther is densely covered with pollen, yet it only forms a single series, and each grain is echinate and distinctly pedicellate, the whole forming a beautiful microscopic object. (*Contributions*

to a Flora of Ceylon.) In Cycads the anthers are sessile, 3- or 4-celled, open vertically, and are scattered over the face of a bract metamorphosed into the hard scale of a cone. Conifers, too, present some singular anomalies, which have been studied by Zuccarini. (See *Ray Reports,* 1845.)

With regard to deviations from the usual mode of dehiscence, Brown observes (*Linn. Trans.* xiii. 214.), "that they are numerous: in some cases consisting either in the aperture being confined to a definite portion,—generally the upper extremity of the longitudinal furrow,—as in Dillenia and Solanum; in the apex of each theca being produced beyond the receptacle of the pollen into a tube opening at top, as in several Heathworts (Ericaceæ) (Plate III. fig. 22.); or in the two thecæ being confluent at the apex, and bursting by a common foramen or tube, as in Tetratheca (see Plate IV. fig. 4.). In other cases a separation of determinate portions of the membrane takes place, either the whole length of the theca, as in Witch Hazels (Hamamelidaceæ) and Berberids, or corresponding with its subdivisions, as in several Laurels (Lauraceæ), or lastly, having no obvious relation to internal structure as in certain species of Rhizophora." In Laurels and Berberids the anthers are technically said to burst by recurved valves (Plate IV. fig. 10, 11.), that is to say, the dehiscence does not take place by a central line, but the whole face of the cell separates from the anther, and curls backwards, adhering to it only at the apex, to which it is, as it were, hinged.

In Rhizophora, above alluded to, the anther is said by Mr. Griffith to be compressed, with the edges anterior and posterior, and to open by the separation of a valve from the sides, when the pollen is seen lying in socket-like excavations, the upper portions of which may be traced on the inner face of the valves. (*Trans. Med. & Phys. Soc. Calcutta*). Mr. Griffith rightly explains this singular structure to be a modification of dehiscence, caused by the adhesion of the valves to each other at the usual line of fissure, and their separation from the connective. It is not therefore quite correct to say that the dehiscence of Rhizophora bears no obvious relation to internal structure; it is of the same nature as that of Laurels,

Berberids, &c., and is analogous to the disarticulation of the valves of Cruciferous plants.

A very singular deviation from the usual structure of the anther occurs in Cryptocoryne ciliata, an Arad, thus described by the late Mr. Griffith:—

"The anthers may, from a very early period, be compared to two cups joined together by their contiguous margins; the wide and open mouth which they present in their mature state, being closed up originally by an extremely fine membrane, lining the cavity of the cup and forming a convexity where it closes in the opening. Within the cavity thus formed the pollen is developed. As the anther increases in size this membrane gradually assumes the form of a cone, which projects in proportion as it increases beyond the margins of the cups or thecæ. At the same time it assumes a yellow tint, by which, chiefly, I am led to think that it lines the entire cavities of the thecæ. The cellular tissue of the thecæ consists of a cutis, which is papillose on the margins of the cup, and an inner series of ovate cells arranged with their long diameters pointing from the axis. On the membrane of these cells very distinct fibres are developed, which almost always have the same direction with the cells. These fibres cross each other at very acute angles, and appear to be incomplete at either end of the cell, in which they are developed. The cone soon becomes more subulate, it remains closed, and is of a yellowish tint. The anthers appear to be fully formed at a time when the spadix is only half developed. At a later period the apex of the cone is open, and through this opening the contents of the thecæ may be squeezed, assuming, from the comparatively small diameter of the apex of the cone, a more or less elongated form. In the instance figured, the length to which they attained was immense. The matter squeezed out resembles exactly the process which originates from most globules of pollen, when acted on by water, and the very great length above noticed, arose probably from the coalition of the processes of several granules occasioned by the pressure exerted." (*Linnæan Transactions*, vol. xx.)

The cells of the anther have frequently little appendages,

as in different species of Erica, when they resemble setæ, aristæ, or crests. (Plate III. fig. 29.)

The anthers are attached to the filament either by their base, when they are called *innate* (Plate III. fig. 27. 21. 23.), or by their back, when they are *adnate* (Plate III. fig. 13.), or by a single point of the connective from which they lightly swing: in the latter case they are said to be *versatile*. This form is common to all true Grasses.

When the line of dehiscence is towards the pistil, the anthers are called by Brown *anticæ*, but by other botanists *introrsæ*, or turned inwards: when the line is towards the petals, they are said by Brown to be *posticæ*, and by other botanists to be *extrorsæ*, or turned outwards.

The *connective* is usually continuous with the filament, and terminates just at the apex of the anther; but in some plants, as Composites, it is articulated with the filament (Plate IV. fig. 5.). In others it is lengthened far beyond the apex (Plate IV. fig. 6. 9.), now into a kind of crest, as in many Gingerworts (Zingiberaceæ); now into a sort of horn, as in Asclepiads; now into a kind of secreting cup-like body articulated with the apex, as in Adenostemon. Very frequently it is enlarged in various ways. For cases of this kind, see Plates III. and IV. Its being sometimes two-lobed, or forked, has been already noticed (Plate IV. fig. 7.).

The *lining* of the anther has received particular illustration from Purkinje, who calls it *endothecium*, and who has found that it consists of that very remarkable kind of tissue, which has been already described under the name of fibro-cellular, (page 51). According to that botanist the forms of this tissue are extremely variable, the vesicles being sometimes oblong, sometimes round, frequently cylindrical, usually fully developed, or, in some cases, merely rudimentary; the vesicles are in some species erect, in others decumbent, but in all cases more or less fibrous. (See Plate I. figs. 4, 13, 14, 15, 18, 19, 20.). For an elaborate treatise on the subject, see Joh. Ev. Purkinje *de Cellulis Antherarum Fibrosis:* Vratislaviæ, 1830, 4to; with eighteen plates.

The stamen deviates in a greater degree than any other

organ from the structure of the leaf, by a modification of which it is produced; and, at first sight, in many cases, it appears impossible to discover any analogy between the type and its modification; as, for instance, between the stamen and leaf of a Rose. Nevertheless, if we watch the transitions which take place between the several organs in certain species, what was before mysterious, or even inscrutable, becomes clear and intelligible. In Nymphæa alba the petals so gradually change into stamens, that the process may be distinctly seen to depend upon a contraction of the lower half of a petal into the filament, and by a development of yellow matter within the substance of the upper end of the same petal on each side into pollen. A similar kind of passage from petals to stamens may be found in Calycanthus, Illicium, and many other plants. Now, as no one can doubt that a petal is a modified leaf, it will necessarily follow, from what has been stated, that a stamen is one also. But it is not from parts in their normal state that the best ideas of the real nature of the stamen may be formed; it is rather by parts in a monstrous state, when reverting to the form of that organ from which they were transformed, that we can most correctly judge of the exact nature of the modification. Take for example that well-known double Rose, called by the French R. Œillet. In that very remarkable variety, the claw of the petals may at all times be found in every degree of gradation from its common state to that of a filament, and the limb sometimes almost of its usual degree of development,—sometimes contracting into a lobe of the anther on one side, or perhaps on both sides,—now having the part that assumes the character of the anther merely yellow,—now polliniferous,—and finally acquiring, in many instances, all the characters of an undoubted though somewhat distorted stamen. Double Pæonies, Double Tulips, and many other monstrous flowers, particularly of an icosandrous or polyandrous structure, afford equally instructive specimens. It is for these reasons that it was stated in the *Outlines of the first Principles of Botany*, p. 307., that "the anther is a modification of the lamina, and the filament of the petiole."

I ought, perhaps, to have put the explanation in a more

extended form. A leaf consists of a midrib, on each side of which is a parenchymatous expansion, consisting of a double stratum of tissue, separated by vessels. In the anther the midrib assumes the form of the connective; the double stratum on each side of the midrib is, at the centre, developed in the form of pollen, and hence the primitive quadrilocular structure of the anther, as above described. The line of dehiscence in ordinary circumstances is the margin of the modified leaf. Schleiden makes this additional remark:—"The normal leaf, as is well known, exhibits upon its upper surface cellular tissue, different in structure from that on the under; to this we find that the pollen of the anterior and posterior cells of the anther corresponds. It may, perhaps, be possible, and certainly would not be uninteresting, to ascertain, by experiment, whether or not the pollen of one of these compartments only possesses the external characters * of pollen, and likewise different functions in the process of impregnation, or whether in diœcious plants one kind would produce male, the other female embryos."

Agardh considers a stamen to be composed of two leaves in a state of adhesion; and that it is in fact a bud axillary to a sepal or petal. This is very nearly the opinion formerly entertained by Wolff. Endlicher adopts this view to a certain extent; and supposes the leaves to be rolled backwards, so that their under surface becomes the polliniferous part. But all this is mere hypothesis, unsupported by evidence, and in opposition to the direct observations of Mirbel and Schleiden. The latter well observes, that the stamens are evidently modified simple leaves, for they constantly appear at a later period than the petals, although they afterwards develope themselves more rapidly; they stand at first higher up upon the axis than the preceding circle of corolline leaves, and they alternate invariably with them.

Such is the structure of the stamens in their perfect state. It often, however, happens that, owing to causes with which

* It is so expressed in the translation in Taylor's Magazine; in the original it is; "ob vielleicht der pollen einer von beiden, nur der form nach pollen sei, und bei der befruchtung sich verschieden verhalte," u. s. w.

we are unacquainted, some of the stamens are developed imperfectly, without the anther and pollen. In such cases they are called *sterile stamens* (*parastemones* Link), and are frequently only to be recognised by the position they bear with respect to the other parts of the flower. Botanists consider every appendage, or process, or organ, which forms part of the same series of organs as the true stamens, or which originates between them and the pistil, as stamens, or as belonging to what Röper calls the *andrœceum*, namely, to the *male system;* and every thing on the outside of the fertile stamens is in like manner often referred to modifications of petals, a remarkable instance of which is exhibited by Passiflora. There is, however, no certain rule by which it can be determined whether such bodies belong to the stamens or petals.

The appearances assumed by these sterile stamens are often exceedingly curious, and generally very unlike those of the fertile stamens; thus in Canna they are exactly like the petals; in Hamamelis they are oblong fleshy bodies, alternating with the fertile stamens; in Pentapetes they are filiform, and placed between every three fertile stamens; in Gingerworts (Zingiberaceæ) they are minute gland-like corpuscles, a very common form (Plate IV. fig. 10. *c.*); in Brodiæa they are bifid petaloid scales; and in Asclepiads they undergo yet more remarkable transformations. Dunal calls these sterile stamens *lepals* (*lepala*); a term which has not yet been adopted.

9. Of the Pollen.

The pollen is the pulverulent substance which fills the cells of the anther. It consists of extremely minute grains, varying in size, and inclosing a fluid containing molecular matter. The pollen-grains are often called *granules*.

It appears to consist of wax, forming a portion of its shell, of globules of oil, and of starch. Dr. H. Giraud has mentioned the existence of potassa in the pollen of Antirrhinum majus; and of raphides, consisting of phosphate of lime, mixed up with the pollen of Tradescantia virginica, and

with that of certain Orchids. According to Fourcroy and Vauquelin, the pollen of the Date tree consists of malic acid, phosphate of magnesia and lime, and also of an insoluble animal matter intermediate between gluten and albumen. Macaire Prinsep has ascertained that the pollen of the Cedar contains malate of potass, sulphate of potass, phosphate of lime, silica, sugar, gum, yellow resin, and a substance which, by its characters, approximated to starch. Being analysed as a whole, it gave per cent., 40 carbon, 11·7 hydrogen, and 48·3 oxygen, but no nitrogen. (*Bibl. Univers.* 1830, p. 45.)

Pollen has been found to contain sugar, a yellow colouring matter, gum, starch, a fixed oil, malic acid, phosphates, and especially a peculiar, azotized, inflammable principle which is insoluble in nearly every liquid and is called Pollenine. (*Girardin Leçons de Chimie Élémentaire,* 3rd edn. p. 839.)

Mr. Herapath gives the following as the results of his examination of the pollen of the white and red lily, and of Cereus speciosissimus:—

	Lilium Bulbiferum (Red Lily.)	Lilium Candidum (White Lily).	Cereus Speciosissimus.
Water	12·650	17·625	15·070
Sugar, and a little malate of potash	14·530	14·285	20·548
Gum and extractive	17·465	18·326	6·392
Albumen	0·873	0·546	.....
Extractive with carbonate, phosphate, and sulphate of lime	1·000	0·921	3·196
Yellow fixed oil	7·590	8·059	.....
Pollenine	43·012	36·936	46·575
Cerin	0·200	0·300	8·219
Resin	a trace	.....	.....
	97·320	96·998	100·000

(*Pharmaceutical Journal,* 1848. *February.*) But we do not see where the starch, which exists in all Pollen, appears. Is it included in his Sugar, or Gum? and what is this Chemist's Extractive?

To this important part of the organisation of perfect plants, attention has been directed with great care and skill by numerous observers of the first class, among whom are especially to be noticed R. Brown, Ad. Brongniart, Fritzsche, Griffith, Mirbel, Mohl, and Schleiden. From their inquiries,

we have arrived at a knowledge of the history of the pollen, notwithstanding its minuteness, from its first secretion to its final destruction, after the important purpose for which it is provided has been attained.

The *origin of the pollen*, according to the testimony of all observers, occurs in the cells of which the anther is composed, and appears to consist in a peculiar organisation of their granular interior. The grains are usually produced in fours, by the bisection of their generating cell in two opposite directions, but are occasionally formed in pairs or singly.

In 1831, Brown speaks thus of the evolution of the pollen of Tradescantia virginica. "In the very early stage of the flower bud, while the antheræ are yet colourless, their loculi are filled with minute lenticular grains, having a transparent flat limb, with a slightly convex and minutely granular semi-opaque disk. This disk is the nucleus of the cell, which probably loses its membrane or limb, and, gradually enlarging, forms in the next stage a grain also lenticular, and which is marked either with only one transparent line, dividing it into two equal parts, or with two lines crossing at right angles, and dividing it into four equal parts. In each of the quadrants a small nucleus is visible: and even where one transparent line only is distinguishable, two nuclei may often be found in each semicircular division. These nuclei may be readily extracted from the containing grain by pressure, and, after separation, retain their original form. In the next stage examined, the greater number of grains consisted of the semicircular divisions already noticed, which had naturally separated, and now contained only one nucleus, which had greatly increased in size. In the succeeding state the grain apparently consisted of the nucleus of the former stage, considerably enlarged, having a regular oval form, a somewhat granular surface, and originally a small nucleus. This oval grain continuing to increase in size, and in the thickness and opacity of its membrane, acquires a pale yellow colour, and is now the perfect grain of pollen." (*On Orchid. and Asclep.* p. 21.)

In 1832, Mirbel examined the development of pollen in the anther of a Gourd. He states that "when the flower-bud

of this plant is about a line in length, each lobe of the anther is entirely composed of cellular tissue, the bladders of which present in general a pentagonal or hexagonal figure more or less regular when cut across. In every cell, without excepting even those which constitute the superficial layer of the lobe, are certain loose particles, of such extreme minuteness that a magnifying power of 500 or 600 diameters is required to examine them satisfactorily. I cannot compare them to anything better than to little transparent bladders, nearly colourless, more or less rounded, and of an equal size. I examined the cells of the lobe of the anther one by one; and I affirm that, at this early period, there is no trace of either the cells of the anther or of the grains of pollen. The whole of the tissue is perfectly uniform. In a flower-bud, but little larger than the first, I remarked on each side of the medial line of the slice a group, consisting of a few bladders, which were rather larger than the others, but otherwise like them. These larger bladders I propose to call *pollen-cells*, seeing that it is in their inside that the pollen is organised. In flower-buds, from $1\frac{1}{2}$ to 2 lines in length, some remarkable changes were observable. The pollen-cells had become larger; their granules were so much multiplied that they were grouped and packed in opaque masses, and wholly filled the cells. These cells and granules together constituted a greyish body, joined to the rest of the tissue by the intervention of a cellular membrane,—a sort of integument which, notwithstanding its organic continuity with the surrounding parts, was readily distinguishable; for while the bladders of the surrounding parts lengthened parallel to the plane of the surface, and to the plane of the base of the anther, those of the integument lengthened from the centre to the circumference. In anthers a little further advanced, the sides of the pollen-cells, instead of being thin and dry as they had previously been, acquired a notable thickness, and their substance, gorged with fluid, resembled a colourless jelly. The cellular integument continued to adhere by its outer face to the lining of the cell of the anther, and by its inner face to the tissue formed by the pollen-cells. Three and a half or four lines of length in the flower-bud corresponded with a phenomenon altogether unexpected. At first the

thick and succulent wall of each pollen-cell dilated, so as to leave a void between its inner face and the granules, not one of which separated from the mass, which proved that a force of some kind held them together. Shortly after four appendages, like knife-blades, developed at equal distances on the inner face of the pollen-cell, and gradually directed their edge towards the centre, so that they began by cleaving the granular mass in four different lines, and finished by dividing it into four little triangular masses; and when the appendages met in the centre they grew together, and divided the cavity of the pollen-cell into four distinct cavities, which soon after rounded off their angles, and in a short time the little granular masses became spherical, like melted lead run into the hollow of a bullet-mould. The partition of the mass thus brought about by the appendages seems to me to indicate that at this period the mass was not protected by a special integument, and that the mutual adhesion of the granules was very weak.

"When things had arrived at this point, the portion of the tissue formed by the pollen-cells separated itself from the surrounding parts, and each pollen-cell became loose, generally in the form of a square parallelopiped with rounded angles; each little mass of granules gained a smooth, colourless, transparent membrane, which was at first membranous, but afterwards became thick and succulent, and soon began to take on the characters peculiar to the pollen of the Gourd. The integument began to bristle with fine conical papillæ; several roundish lids were traced out here and there on its surface; it hardened, became opaque, assumed a yellow colour, ceased to grow, and attained its perfect maturity." Mirbel adds to this highly interesting statement, that he finds in the generality of plants that the mode of forming the pollen is much the same as in the Gourd.

Observations upon the same subject by Professor Mohl were published in Berne, in 1834. The principal points of novelty in regard to the development of the pollen are, that, 1. The union of pollen-grains in fours is sometimes permanent, sometimes very temporary. 2. That the four are sometimes placed upon the same plane, sometimes in the

same relation to each other as the four angles of a cube. 3. That the original number of cohering grains is in most species of Inga, Acacia, and Mimosa, from eight to sixteen. 4. That the external coat of the pollen-grain is not an uniform membrane, analogous to that of a simple cell, but an organ composed of numerous cells like the integument of an ovule, although it appears in some cases to be simply granular, and in others to be almost homogeneous. This last idea is sharply attacked by Mirbel (*Ann. Sc.;* n. s., IV. 1.), who insists upon the external skin of the pollen-grain being simple in all cases.

Mr. Griffith, in November 1836, published some curious observations upon this subject, the result of which is, that in Pardanthus chinensis the pollen is developed in the midst of a solid grumous semiopaque mass, forming at a very early stage the contents of one of the four cells of the anther; that subsequently the grumous mass becomes cellular, the cells having undergone some separation, and consisting of a hyaline membrane containing a smaller mass of granular molecular matter. Later still, each cell, which has acquired an orange colour, presents traces of division into four, often into three, very rarely into two portions, the division being more distinct towards the circumference of each cell, and the smaller masses being each enclosed in a proper cell, but without having undergone any separation. Eventually each of the divisions becomes a pollen-grain. "The young grains are oblong-ovate, flattened on their contiguous or inner faces, and open along the centre throughout the whole length of their outer faces. They are even at this period reticulated, and have rather a papillose appearance, and are lined by an inner membrane in the form of a hyaline sac, which bulges out slightly along the opening just mentioned."

According to Schleiden, the difference between ordinary pollen and that found in *masses* in Asclepiads and Orchids consists in this, that the enveloping cells in common cases *are*, and in the two others *are not*, absorbed. "This same condition may be seen as a temporary stage in the development of Picea and Abies, in the months of January and February, in Pinus in February and March, in which a loose

waxy pollen mass may be found embedded in each division of the anther. At a somewhat later period we may see the four cells in Picea and Abies, in which the four pollen-grains lie closely united; and it offers a pleasing spectacle under the microscope to observe each grain expand itself by the absorption of water until it bursts its case in order to escape, leaving the four cells emptied of their contents."

Link supposes the cellular substance in which pollen is generated to be semiorganic, and calls it *collenchyma*, considering with me that it is what forms the appendage of the pollen masses of Orchids. But it can hardly be called semiorganic, especially if it is examined in Polystachya ramulosa.

It also appears from Mr. Francis Bauer's observations, that the masses of pollen of both Asclepiads and Orchids in the most solid state, are truly cellular, the grains of pollen being contained in cavities, the walls of which are either separable from each other, as in some Orchids, or are ruptured without a separation of the cavities, as in Asclepiads. (See the *Observations on Orchidaceæ and Asclepiadaceæ*, before referred to.) It does not, however, follow that because pollen is engendered in the interior of cells, its grains must therefore adhere originally by an umbilicus; and in fact the part so described by Turpin has no existence.

When the pollen-grains are fully formed they are generally discharged at once, upon the dehiscence of the anther. But in some Arads, which emit their pollen by a hole in the apex of their anther, the formation or development of pollen must be going on for a considerable time after the first emission. A single anther continues to secrete and discharge pollen, till, as Brown remarks, the whole quantity produced greatly exceeds the size of the secreting organ.

The *surface* of the pollen is commonly smooth. In some plants it is hispid, as in the Gourd and Ipomœa purpurea; in others it is covered with strong points, as the Althæa frutex (Hibiscus syriacus); in Jatropha panduræfolia it is granular; in many Labiates, banded; in Passiflora, reticulated; in Geranium sylvaticum, crested; in Armeria vulgaris, polygonal,

with crested angles; among it occur some of the most beautiful microscopical appearances in the vegetable kingdom. In all cases, where there are asperities of the surface or angles in the outline, pollen is asserted by Guillemin to have a mucous surface, which was first observed in Proteads by Brown. But Mohl finds that the presence of mucosity upon pollen is a constant character, at least when the grains first quit the anther; and that a power of secreting a viscid substance is one of their functions when perfectly smooth, as well as when covered with points and inequalities. He, however, admits that hispid pollen is generally more viscid than that which is smooth.

The *figure* of the granules is various; most frequently it is spherical or slightly oblong. Many other forms have, however, been described. The cylindrical exists in Anethum segetum, and in a very remarkable degree in Spiderwort (Tradescantia virginica,) where the grains become curved: in Bladder Senna (Colutea arborescens), they were observed by Guillemin to be nearly square; in Lavatera acerifolia to be oval, much attenuated to each end; in Œnothera they are triangular, with the angles so much dilated as to give the sides a curved form; in Jacaranda tomentosa I have remarked them to be spherical, with three projecting ribs tapering to either apex; in some Composites (Cichoraceæ) the granules are spherical with facettes; in Teazelworts (Dipsacaceæ) a depressed polyedron; in Scabiosa caucasica, patelliform and angular. In numerous plants it is oval, with a furrow on one side, like a grain of wheat; in Thunbergia fragrans, Mimulus moschatus, &c., it is strongly ribbed, as if formed of many folds; in Morina persica, cylindrical, with a narrow neck rising abruptly from each side; in Scolymus, Scorzonera, &c., it is a polygon, with crested angles; and of all these there are numerous modifications, some of which are represented in Plate IV. See *Elements of Botany*, p. 84, fig. 173, for numerous figures of pollen-grains.

In consequence of the great diversity of forms observable in pollen, it has been supposed that it might be employed in the definitions required for systematic botany; and Messrs. Guillemin and Adolphe Brongniart have stated that plants of

the same family have similar pollen, adducing as instances Grasses (Graminaceæ), Sedges (Cyperaceæ), Daphnads (Thymelaceæ), Proteads, &c., &c. But Mohl, who has inquired into this part of the subject in a most elaborate manner, declares that pollen varies extremely in form, not only in genera of the same family, but also in species of the same genus; and that it even occurs in some plants that the same anther contains grains, "de formation assez diverse." The more or less complex structure of the pollen is not in relation to the more or less elevated station of a plant in the scale of development; but the same form is found in families so different, that they are separated by every other point of structure.

The *shell of the pollen-grain* appears to the observer who examines it with low magnifying powers, as if it were simple. But it has been ascertained to consist in the greater part of plants of two or even three membranes, of which the outer (*extine*) is thicker than the inner (*intine*), the latter being hyaline, extensible, and of extreme tenuity, not colourable by iodine, and destructible by concentrated sulphuric acid. Mohl considers the extine to be in all cases composed of minute grains, or cells, held together by organic mucus: that it is often cellular there is no doubt; he refers, in proof of the correctness of this opinion, to cases where, as in Pitcairnia latifolia, the coating is manifestly cellular in the middle of the pollen-grain, but becomes granular at the extremities. He also states, that in other cases the points forming granulations become less and less, till, at last, the membrane becomes almost entirely smooth and uniform, and is extremely like the membrane in the common cells of plants; as in Allium fistulosum, Araucaria imbricata, &c. Mirbel, however, disputes the cellularity of the extine; and Fritzsche, in his latest work, asserts that it unquestionably is sometimes a simple membrane (p. 30.). The intine has the power of absorbing water with great force, so that immediately upon being exposed to the action of a fluid it swells, and eventually bursts, discharging its contents; in general the extine extends as well as the intine, and then the organic difference between them is not observable: but in the Yew

(Taxus,) Juniperus, Cypress (Cupressus,) Arborvitæ (Thuja,) the outer membrane has, as Mohl states, so little extensibility, that it is torn irregularly, and the inner membrane protrudes beyond the crevices, and, swelling more and more, generally disengages itself from the extine. It sometimes happens that the inner membrane protrudes beyond the outer shell, in the form of a short sac or tube: this phenomenon may be produced artificially at will by placing the pollen-grain in weak nitric or sulphuric acid; but it is quite a distinct emission from that of the pollen-tubes hereafter to be noticed.

A third membrane, intermediate between the extine and intine, was first noticed by Mohl in the pollen of the Yew (Taxus), Juniperus, Cupressus, and Thuja. Fritzsche calls it the *Exintine*, and finds it not only in these plants, but also in Pinus, the Gourd, (Cucurbita Pepo), and Tigridia Pavonia, and considers it probably a common structure. The same minute observer speaks of four coatings to the pollen of Clarkia elegans, calling the fourth, which is next the extine, the *Intexine;* he also finds the same structure in other Onagrads.

Mohl names Asclepiads as those only in which pollen has but one tunic; but Fritzsche asserts that these plants have both an extine and intine, and he figures them in Asclepias syriaca; he adds, that in Caulinia fragilis, Zannichellia pedunculata, Zostera marina, and Naias minor, the pollen has really nothing but the intine present.

There are few forms of pollen in which the extine presents the appearance of a vesicle completely closed. In many cases the grains are marked by a longitudinal furrow on one side, and look when dry like a grain of wheat. Mr. Griffith has shown, as is above stated, that this appearance is caused by a fissure in the extine, and if such pollen is put into water the fissure becomes less visible. The presence of one or more such clefts is of common occurrence; and have been supposed to be openings through the extine down to the intine; Mohl, however, considers them not to be really openings, but only extremely thin spaces in the extine. Fritzsche calls them pores, and regards them as certainly openings. Instead of

slits many kinds of pollen have circular holes, varying in number, in different species, from one to an indefinite quantity in the Hollyhock (Alcea rosea). Under these holes Fritzsche finds small, plano-convex, lenticular, intermediate bodies (*zwischenkörpern*), lying between the extine and the intine, with their convexity reposing upon the latter; he represents them as particularly large in some Mallowworts.

The *colour* of pollen is chiefly yellow. In Epilobium angustifolium and many Polemoniads it is blue; in Verbascum it is red; and it occasionally assumes almost every other colour, except green.

The matter contained in the granules is called the *fovilla*. Under common magnifiers it appears like a turbid fluid; under glasses of greater power it has been found to consist of a multitude of particles moving on their axes with activity, of such excessive minuteness as to be invisible unless viewed with a magnifying power equal to 300 diameters, and measuring from the 4000th or 5000th to the 20,000th or 30,000th of an inch in length. This motion was first distinctly noticed by Gleichen; but it seems to have escaped the recollection of succeeding botanists until the fact was confirmed by Amici, who some time before 1824 saw and described a distinct, active, molecular motion in the pollen of Portulaca oleracea. In 1825 the existence of this motion was confirmed by Guillemin, who ascertained its presence in other species. In June 1827, I was shown the motion by Dr. Brown, who subsequently published some valuable observations upon the subject, without, however, noticing those of either Amici or Guillemin. The most important addition that was made by Brown to the knowledge that previously existed, consisted in the discovery of the presence of two kinds of active particles in pollen; of which, one is spheroidal, extremely minute, and not distinguishable from the moving, ultimate, organic molecules common to all parts of a vegetable; the other, much larger, often oblong, and unlike any other kind of particle hitherto detected in plants. Clarkia pulchella, and some other Onagrads plants, show this difference, as well as the motion,

in a very conspicuous manner. In consequence of their manifest motion it has been conjectured that the larger particles of the fovilla were the incipients of the embryo, and that it is by the introduction of one or more of these into the ovule that the act of impregnation is accomplished by the deposit of a rudimentary embryo in the ovule. But both Fritzsche and Mohl agree in considering many of the smaller particles of the fovilla as minute drops of oil: the molecular motion has been ascribed to currents in the fluid, in which the fovilla is suspended, and which, according to Fraunhofer, no precautions can possibly prevent; and, what is more important, the larger particles become blue upon the application of iodine, without however losing their property of motion, as Fritzsche has shown: they are therefore starch.

When the pollen falls upon the stigma it emits a fine transparent tube, which is a prolongation of the intine, and down which the fovilla passes until the grain is emptied. The *pollen-tube* thus formed was first observed by Amici, and is now known to be constantly produced at the period of impregnation. Of the important offices these tubes have to perform an account will be given in Book II. Chap. vi.

For further information concerning pollen the reader is referred to the following works:—

1. Fritzsche, *De Plantarum Polline:* Berolini, 1833. This ingenious observer found that several modes of examining pollen are preferable to those usually employed: in particular he recommends the employment of sulphuric acid, in the proportion of two parts of concentrated acid to three parts of water, for the purpose of viewing the pollen by transmitted light; by this means it is rendered transparent, and the spontaneous emission of pollen tubes is effected. In cases of very opaque pollen he employs oil instead of diluted acid, and he finds it renders an object more transparent than the acid itself; and in other cases, where the coat of the pollen is either too much or too little transparent to show the apertures in its sides, he finds a solution of iodine in weak spirits of wine extremely useful.—2. Mohl, *Sur la Structure et les Formes des Grains de Pollen:* translated from the German in

the *Annales des Sciences*, n. s., III. 148.—And, 3., to Fritzsche, *Ueber der Pollen:* 4to., St. Petersburgh, 1837, with thirteen coloured plates. In this last excellent work all the refinements of optical instruments and chemical manipulation have been employed in the investigation of the subject.

10. Of the Disk.

By this term are meant certain bodies or projections, situated between the base of the stamens and the base of the ovary, but forming part with neither; they are referred by the school of Linnæus, along with other things, to nectarium: Link calls them *sarcoma* and *perigynium;* and Turpin, *phycostemones.* Their most common form is that of a fleshy ring, either entire or variously lobed, surrounding the base of the ovary (Plate V. fig. 4. *e*, 8. *d.*) as in Lamium Cobæa, Gratiola, Orobanche, &c.; in Gesnerads and Proteads the disk consists of fleshy bodies of a conical figure, which are usually called *glandulæ hypogynæ.* It occasionally assumes the appearance of a cup, named by De Candolle, in Pæonies and Aconites, *lepisma,* a bad term, for which it is better to say *discus cyathiformis.* In flowers with an inferior ovary (Plate V. fig. 9. *c*, 7. *c.*) the disk necessarily ceases to be hypogynous, and generally also to appear in the form of scales. In Composites it is a fleshy solid body, interposed between the top of the ovary and the base of the style; and has given rise, when much enlarged, to the unfounded belief in the existence of a superior ovary in that order, as in Tarchonanthus. In Umbellifers (Apiaceæ) it is dilated, and covers the whole summit of the ovary, adhering firmly to the base of the styles; by Hoffmann it is then called *stylopodium,* a word which is seldom used.

It is the general opinion that a disk is really only a rudimentary state of the stamens; and it is thought that proofs of the correctness of this hypothesis are to be found in the frequent separation of the cyathiform disk into bodies alternating with the true stamens, as in Gesnera; in its resemblance in Parnassia to bundles of polyadelphous stamens; and particularly in the fact noticed by Brown, that an anther is

occasionally produced upon the highly developed disk of Pæonia Moutan. To which may be added the observation of Dunal, that half the disk of Cistus vaginatus occasionally turns into stamens. (*Considerations,* &c., p. 44.)

Like the petals, sepals, and stamens, the disk always originates below the pistil; but it often contracts an adhesion with the sides of the calyx, when it becomes *perigynous,* as in Amygdalus; or with both the calyx and the sides of an inferior ovary, when it becomes *epigynous,* as in Umbelliferous plants.

11. Of the Pistil.

The last organ to enumerate in the flower is that which constitutes the *female system,* or *gynæceum* of Röper, and which is usually called the *pistil.* In all cases it occupies the centre of the flower, terminating the axis of growth of the peduncle: and is consequently the part around which every other organ, without exception, is arranged in hermaphrodite structures.

It is distinguished into three parts; viz. the *ovary* (Plate V. fig. 7. *a.*), the *style* (fig. 7. *f.*), and the *stigma* (fig. 7. *g.*).

The OVARY, called germen by Linnæus, is a hollow case placed at the base of the pistil, enclosing the *ovules,* and always containing one or more *cells* or cavities. It is the part which ultimately becomes the fruit; and consequently, whatever may be the structure of the ovary, such must necessarily be that of the fruit: allowance being made, as will hereafter be explained, for changes that may occur during the progress of the ovary to maturity.

Notwithstanding what has been stated of the pistil constantly occupying the centre of the flower, and being the part *around* which all the other parts are arranged, an apparent exception exists in those flowers the calyx of which is said to be superior (Plate V. fig. 7 & 9.), as the Apple blossom. In this instance, the ovary seems to originate *below* the calyx, corolla, and male system; on which account it is said to be *inferior* in such cases, while in the opposite state it is called

superior. But, in reality, the inferior ovary is only so in consequence of the tube of the calyx *contracting an adhesion with its sides;* and such being the case, the exactness of the description of the constant place of the pistillum as above is unshaken. This is proved in many ways. Among Saxifrages, the genus Leiogyne has the ovary superior; in Saxifraga itself the calyx partially adheres to the sides of the ovary, which then becomes half inferior; while in Chrysosplenium the union between the calyx and ovary is complete, and the latter is wholly inferior. Again, in Appleworts (Pomaceæ) the ovaries partially cohere with the calyx in Photinia, completely in Pyrus, and by their backs only in Cotoneaster; whence the ovary is half superior in the first instance, quite inferior in the second, and what is called *parietal* in the third. (Botanists call anything *parietal* which arises from the inner lining or wall of an organ; thus in Cotoneaster the ovaries are parietal, because they adhere to the inner lining of the calyx, and in Papaver the placentæ are parietal because they originate in the inner lining of the fruit.)

Sometimes the ovary, instead of being sessile, as is usually the case, is seated upon a long stalk; as in the Passion flower and the genus Cleome. This stalk is often called the *thecaphore* or *gynophore* (also *basigynium* or *podogynium*); but it is obviously analogous either to the petioles of carpellary leaves or to an internode, and the application of a special term to it appears unnecessary. Cassini calls the elongated apex of the ovary of some Compositæ, *le plateau.*

That part of the ovary from which the ovules arise is called the *placenta* (*trophospermium,* Richard; *spermaphorum, colum, receptacle of the seeds*). It generally occupies the whole or a portion of one angle of each cell (Plate V. fig. 1. *e.*, 2. *c.*, &c.), and will be spoken of more particularly hereafter. It is sometimes lengthened in the form of a little cord, as in the Hazel nut, and many Crucifers: it is then called the *umbilical cord* (*funiculus umbilicalis, podospermium*).

The swelling of the ovary after fertilisation is termed *grossification.*

The *style* (*tuba* of old authors) is that elongation of the

ovary which supports the stigma (Plate V. fig. 7. *f.*). It is frequently absent, and then the stigma is sessile: it is not more essential to a pistil than the stalk to a leaf, or the claw to a petal, or the filament to a stamen. Anatomically considered, it usually consists of a column of one or more bundles of vascular tissue, surrounded by or enclosing cellular tissue; the former communicating on the one hand with the stigma, and on the other with the vascular tissue of the ovary. It is usually taper, often filiform, sometimes very thick, and occasionally angular: rarely thin, flat, and coloured, as in Iris and in Canna. In some plants it is continuous with the ovary, the one passing insensibly into the other, as in Digitalis; in others it is articulated with the ovary, and falls off, by a clean scar, immediately after fertilisation has been accomplished, as in the genus Scirpus. Its usual point of origin is from the apex of the ovary; nevertheless, cases occur in which it proceeds from the side, as in Alchemilla, or even from the base, as in Labiates and Borageworts. In these cases, however, it is to be understood that the geometrical and organic apices are different, the latter being determined by the origin of the style. For this reason, when the style is said to proceed from the side or base of the ovary, it would be more correct to say that the ovary is obliquely inflated or dilated, or that it is gibbous at the base of the style.

There is no doubt that the style is also, in some cases, a mere process of the placenta, wholly free from the carpellary leaves, and not even guarded by an extension of their points. This curious fact is conclusively established by Babingtonia Camphorosmæ, in which, as I have shown in the *Botanical Register*, the style proceeds directly from the placenta itself, and does not even touch the carpels, *but is protruded through a hole in the vertex of the ovary.* I had previously noticed an analogous fact in certain species of the genus Impatiens, in the *Botanical Register* for 1840.

In Impatiens macrochila it was shown that the style is surrounded below its apex by five points, which are evidently continuations of the backs of the carpels. These points were stated to be the points of carpellary leaves, which, in such

plants, are separate from the placenta, and are merely pressed down upon it, so as to cover the ovules, thus confirming the accuracy of the views concerning placentation held by Schykofsky and Schleiden. Upon that supposition the upper part of the style, and the stigmas, were assumed to be the naked apex of the placenta, prolonged beyond the carpellary leaves. The consequence of that hypothesis was, that the conducting tissue of the style would be, in most cases, an extension of the placenta. That being admitted, the indusium of Goodeniads, and, *à fortiori*, the well known rim found upon the stigma in Heathworts (Ericaceæ) would be the expanded end of the carpellary leaves, while the stigma of those plants is also the upper end of their placenta. To this I might have added Cranesbills (Geraniaceæ), in which the carpellary part of the style hardens and rolls up, eventually leaving the prolongation of the placenta as a distinct beak. Such examples certainly justify the assertion that, in numerous cases, the style is formed by the matter of the placenta. Griffith seems to have entertained some similar idea when, in his treatise on Loranthus, &c. in the *Linnæan Transactions*, vol. xix., he spoke of the "intimate relations between the placenta and stigmatic canal."

The surface of the style is commonly smooth; but in Composites, Bellworts (Campanulaceæ) and others, it is often closely covered with hairs, called *collectors*, which seem as if intended as brushes to clear the pollen out of the cells of the anthers. In Lobelia these hairs are collected in a whorl below the stigma. In Goodeniads the style expands at its upper end into a cup, or indusium, surrounding the stigma. (Plate V. fig. 13. *b*.). Many styles which appear to be perfectly simple, as for instance those of the Primrose, the Lamium, the Lily, or the Borage, are in reality composed of several grown together; as is indicated by the lobes of their stigma, or by the number of cells or divisions of their ovary. In Malva an example may be seen of a partial union only of the styles, which are distinct upwards, but united below. In speaking of styles in this latter state, botanists are accustomed to describe them as *divided* in different ways, which is manifestly an inaccurate mode of expression.

The *stigma* is the upper extremity of the style, without epidermis; in consequence of which it has, almost uniformly, either a humid or papillose surface. In the first case it is so in consequence of the fluids of the style being allowed to flow up through the intercellular passages of the tissue, there being no cuticle to repress and conceal them; in the latter case the papillæ are really the rounded sides of vesicles of cellular tissue. When perfectly simple, it is usually notched on one side, the notch corresponding with the side from which the placenta arises: see the stigma of Rosa, Prunus, Pyrus, and others. If it belongs to a single carpel, it is either undivided, or its divisions, if any, are placed side by side, as in Spurgeworts (Euphorbiaceæ), Crocus, &c.; but if it is formed by the union of the stigmas of several carpels, its lobes are either opposite each other, as in Mimulus, or placed in a whorl, as in Geranium. Such being the case, it is a general law that an apparently simple ovary, to which more than two opposite stigmas belong, is really of a compound nature; but, when the stigma of a simple carpel is two-lobed, the arms are often placed exactly opposite each other, as in Composites, Grasses, &c., and then the apparent number of the stigmas is not the real number.

Dr. Robert Brown has the following observations on this subject:—"On the subject of the origin and type of Stigma, my first observation is, that the style, where present, can only be regarded as a mere attenuation, in many cases very gradual, of the whole body of the ovarium. Hence the idea naturally suggests itself, that the inner margins of the carpel, which in the lower part are generally ovuliferous, in the upper part perform the different, though in some degree analogous, function of stigma. As the function, however, of this organ implies its being external, and as in different families, genera, and even species, it has to adapt itself to various arrangements of parts destined to act upon it, corresponding modifications of form and position become necessary; hence it is frequently confined to the apex, and very often, especially in the compound ovarium with united styles, appears to be absolutely terminal.

In such cases, as it must always include and be closely

approximated to all the vascular cord of the axis, it has by some botanists been considered as actually derived from it, which it is, however, only in the same manner as the marginal placentæ are derived from the axis of the carpel. But according to the notion now advanced, each simple pistillum or carpel has necessarily two stigmata, which are to be regarded, not as terminal, but lateral.

That the stigma is always lateral may be inferred from its being obviously so in many cases; and in one genus at least, Tasmannia, it extends nearly the whole length of the ovarium, so as to be commensurate with and placed exactly opposite to the internal polyspermous placenta.

That the stigma is always double appears probable, from those cases in which it is either completely developed, as in the greater part of Gramineæ where the ovarium is simple; in the compound ovarium in Urena; and from those in which the development, though less complete, is still sufficiently obvious, as in many Euphorbiaceæ and in several Irideæ. This degree of development, however, is comparatively rare, confluence between the two stigmata of each carpel being the more usual structure; and in the compound pistillum a greater degree of confluence often takes place in the stigmata than in the placentæ;—a fact, which in all such cases is obviously connected with adaptation of surface to the more complete performance of function."

Nothing is, properly speaking, stigma, except the secreting surface of the style; it very often, however, happens, that the term is carelessly applied to other portions of the style. For example, in the genus Iris, the three petaloid lobed styles in the centre are called stigmata; while the stigma is in reality confined to a narrow transverse humid space at the back of each style: in Labiates, Bentham has shown that what is called a two-lobed stigma, is a two-lobed style, the points only of the lobes of which are stigmatic: and in Lathyrus, and many other papilionaceous plants, Linnean botanists call the hairy back of the style the stigma; while, in fact, the latter is confined to the mere point of the style.

Nevertheless, there are certain stigmas in which no denuded or secreting surface can be detected. Of this nature is that

of Tupistra, in which the apparent stigma is a fungous mass with a surface of the same nature as that of the style; in such a stigma the mode of fertilisation forms an interesting problem, which botanists have yet to solve.

The centre of a stigma consists of tissue of a peculiar character, which communicates directly with the placenta, and which is called the *conducting tissue*. It is more lax than that which surrounds it, and serves for the conveyance of the fertilising matter of the pollen into the ovules. Schleiden says, that, as a style is a portion of a leaf rolled up, or formed by a union of the edges of many leaves (as will be presently shown), the centre of the style must answer to the epidermis of the upper side of such leaf, and therefore this epidermis, modified, constitutes the *conducting tissue*. If the convolution or approximation of the carpels is very complete, the tissue will be a mere thread; but if it be imperfect, as in Orchids, &c., the tissue will form the lining of a funnel-shaped passage from the stigma to the cavity of the ovary. But if, as I hope to have proved by the succeeding observations, the conducting tissue and the true stigmatic surface are really an extension of the placenta itself, then Schleiden's hypothesis requires to be modified or wholly abandoned.

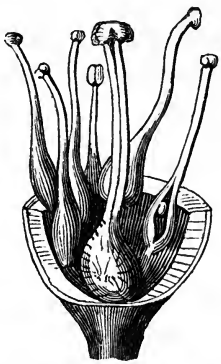
11*. Theoretical Structure of the Pistil.

The foregoing is the common practical view that is taken of the more remarkable peculiarities in the female system of plants. This part, however, fills so important an office in the functions of vegetation, is so valuable as a means of scientific arrangement, and is liable to such a great variety of modifications, that it is also necessary to regard it in another and more philosophical point of view. For we have yet to consider the structure of the compound pistil; to understand the exact nature of its cells, and dissepiments, and placentæ, and the precise relation that these parts bear to each other; and also to prove that the necessary consequence of the laws under which pistils are constructed is, that they can be subject to only a particular kind of modification,

within which every form must absolutely, and without exception, fall. This inquiry would, perhaps, be less important, if the structure of the pistil were regular and uniform; but its numberless anomalies render it one of the most difficult but essential subjects for a student to investigate.

In the days of Linnæus and Gærtner, and even in those of the celebrated L. C. Richard, nothing whatever was known of this matter, and consequently the writings of those carpologists are a tissue of ingenious misconceptions. Nor did the subject become at all intelligible, notwithstanding the writings of Wolff, until the admirable treatise upon Vegetable Metamorphosis, which had been published by Goethe in 1790, but which had long been neglected, was again brought into notice, and illustrated by the skilful demonstrations of De Candolle, Turpin, Du Petit Thouars, and others.

121



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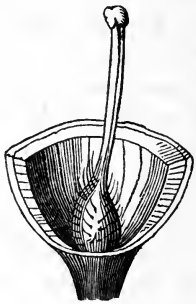


According to these writers, the pistil is either the modification of a single leaf (*fig.* 122.), or of one or more whorls of such leaves (*fig.* 121.), which are technically called *carpels*. Each carpel has its own ovary, style, and stigma, and is formed by a folded leaf, the upper surface of which is turned inwards, the lower outwards, and the two margins of which develope one or a greater number of buds, which are in a rudimentary state, and are called the ovules.

A clear idea of the manner in which this occurs may be obtained from the carpel of a double cherry, in which the

pistil loses its normal carpellary character, and reverts to the structure of the leaf. In this plant the pistil is a little contracted leaf, the sides of which are pressed face to face, the midrib elongated, and its apex discoloured, or a little distended. If we compare this with the pistil of a single cherry, the margins of the leaf with the ventral suture, the elongated midrib with the style, the discoloured distended apex with the stigma, they will be found to correspond exactly.

In this case there is an indisputable identity of origin and nature between the ovary and the blade of a leaf; between the little suture that occupies one angle of the carpel of a cherry, and the line of union of the two edges of the leaf; and between the elongated midrib, with its distended apex, and the style and stigma at least in part. There can be no doubt that the plan of many carpels is the same; so that the ovary is in such cases the blade of a leaf, the style an elongated midrib, and the apparent stigma the apex of the latter.

Such being the origin of the carpel, its two edges will correspond, one to the midrib, the other to the united margins of the leaf. These edges often appear in the carpel like two sutures, of which that which corresponds to the midrib is called the *dorsal,* that which corresponds to the united margins is named the *ventral, suture.*

It is often at some part of the ventral suture that is formed the *placenta,* which is a copious development of cellular substance, out of which the ovules or young seeds arise. It, the placenta, is usually connected with both margins of the carpellary leaf: but, as they are generally in a state of cohesion, there appears to be but one placenta; nevertheless, if, as sometimes happens, the margins of the carpellary leaf do not unite there will in such cases be two obvious placentæ to each carpel. Now, if the stigma is the termination of the dorsal suture, it will occupy the same position as that suture with regard to the two placentæ; consequently the normal position of the two sutural placentæ of a single carpel will, if they are separate, be right and left of the stigma.

Pistils consisting of but one carpel are simple; of several, are compound. If the carpels of a compound pistil are distinct entirely or in part, they are *apocarpous,* as in Caltha; if

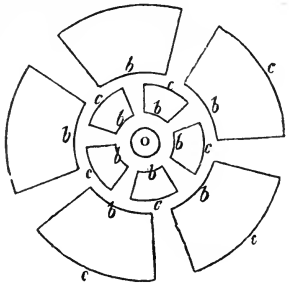
they are completely united into an undivided body, as in Pyrus, they are *syncarpous*. That syncarpous pistils are really made up of a number of united carpels is easily shown, as Goethe has well remarked, in the genus Nigella, in which N. orientalis has the carpels partially united, while N. damascena has them completely so; in the latter case, however, the styles are distinct. They and the stigmas are all consolidated in a single body, when the pistil acquires its most complete state of complication, as in the Tulip; which is, however, if carefully examined, nothing but an obvious modification of such a pistil as that of Nigella damascena.

This important conclusion is deducible from the foregoing considerations: viz., that, as the carpels are modified leaves, they are necessarily subject to the same laws of arrangement, *and to no others,* as leaves developed around a common axis upon one or several planes. For no axiom appears more incontestable in botany, than that all modifications of a given organ are controlled essentially in the same way, and by the same influences, as the organ itself in an unmodified state; and hence every theory of the structure of fruit which is not reducible to that which would be applicable to the structure of whorls of leaves is vicious of necessity. I shall proceed to demonstrate the perfect accordance of the carpellary theory of structure in every point with these principles.

Let it be assumed that the placenta arises from the two margins, either distinct or combined, of a leaf folded inwards. When a leaf is folded inwards, its margins will point towards the stem or axis around which it is developed; and in a whorl of leaves such inflected margins would all be collected round a common centre; or, if the axis were imaginary, in consequence of the whorl being terminal, would be placed next each other, in a circle of which the back of the leaves would represent the circumference. Therefore the placentæ will always be turned towards the axis, or will actually meet there, forming a common centre; and, which is a consequence of this law, if one carpel only, with its single placenta, be formed in a flower, the true centre of that flower will be indicated by the side of the carpel occupied by the placenta. Proofs of this may be found in every blossom:

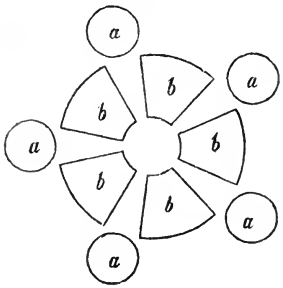
but particularly in such as, habitually having but one carpel, occasionally form two, as the Wistaria sinensis, Alchemilla arvensis, Cerasus acida, &c.; in these the second carpel, when added, does not arise by the side of the first, but opposite to it, the face of its placenta being in front of that of the habitual carpel. A fourth proof of this usual direction of the placentæ towards the axis is afforded by those pistils in which a great number of carpels is developed in several rows, as in the Strawberry and the Ranunculus: in all these the placentæ will be, without exception, found directed towards the axis, and consequently towards the back of every row, except the inner. For example, in the following diagram (123.), let o be the axis, *b b* placentæ, *c c* the backs

fig. 123.



of carpels; the placentæ, *b b*, of the inner row will be next the centre o; the placentæ, *b b*, of the second row will be next the backs, *c c*, of the first row; and so on.

fig. 124.



If the order of development of leaves were exactly followed in that of the stamens and carpels, it would happen that the

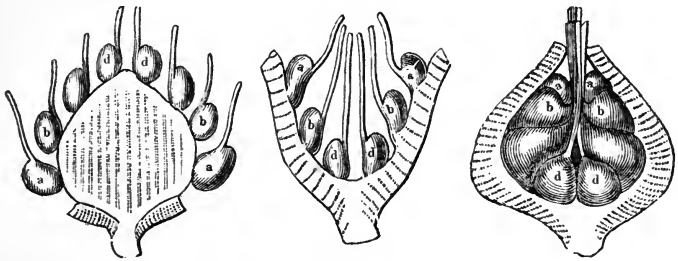
latter would be invariably alternate with the inner row of stamens; for, if *a a* (*fig.* 124.) are the stations of five stamens, *b b* would be the situations of the carpels: this relative position is therefore considered the normal one, and is in fact that which usually exists in perfectly regular flowers; but as all the parts of a flower, in consequence of the non-development of some parts, or the excessive development of others, are subject to deviations, either real or apparent, from what is considered their normal state, it frequently happens that the carpels either bear no apparent relation to the stamens or are opposite to them. In papilionaceous plants, for example, where only one carpel is present, it is difficult to say that it bears any exact relation to the stamens, although it is probable that its position is really normal with regard to them; and so also in rosaceous plants, with numerous carpels, no exact relation can be proved to exist between the latter and the stamens, unless it may be said to be indicated by those genera, such as Spiræa, in which the carpels are reduced to five; and, finally, in such plants as Delphinium, in which the carpels are three, while the floral envelopes and male system are divided upon a quinary plan, it is manifest that no alternation can exist between the stamens and carpels.

As the sepals and petals most commonly consist each of a single whorl of parts, so the pistil is more frequently composed of one whorl of carpels than of more. There are, however, certain families in which several whorls are produced one within the other, as in Fragaria, Ranunculus, Magnolia, Anona, and the like. In these cases it mostly happens that the carpels are either entirely separate or nearly so; but it sometimes is found that syncarpous pistils are habitually produced with more than one whorl of carpels, and consequently of cells, as in Nicotiana multivalvis, and some varieties of the genus Citrus. In such instances the placentæ of the outer series will necessarily be applied to the backs of the inner series, as has been just demonstrated.

This mutual relation of the different rows of carpels is sometimes observed when the receptacle from which they arise is either convex or concave: in the former state the outer series will obviously be lowermost, and in the latter

uppermost; a circumstance that leads to no intricacy of structure when the carpels are distinct, but which may cause an exceedingly anomalous structure in syncarpous pistils, especially when accompanied by other unusual modifications.

125 126 127



There can be no doubt that the true nature of the composition of the pomegranate is to be explained upon this principle. In order to make these considerations more clear, let *figs.* 125, 126, and 127. represent—*fig.* 125. a convex receptacle, with distinct carpels; *fig.* 126. a concave one, with the same; and *fig.* 127. a concave one, with the carpels consolidated. In these, *a a* are the outer row of carpels, *b b* the next, and *d d* the central row. The relative position of these, as the receptacle is convex or concave, will now be apparent.

I have stated that the placenta, however simple it may appear to be, is usually produced by the union of two united margins of a carpellary leaf: it is, therefore, essentially double; and, accordingly, we find that in polyspermous ovaries the ovules are almost always arranged in two rows, as in the Pea and Bean, the Quince, the Pæony, &c.

But there are exceptions to this rule. In *Taylor's Magazine* for Nov., 1837, I have shown that in Broomrapes (Orobanchaceæ) the placentæ undoubtedly arise from the face of the carpel. That the capsule of such plants consists of two carpels standing right and left of the axis of inflorescence, and with the margins not inflected in the form of dissepiments, is incontestable. Yet in Orobanche and Phelypæa the capsule has the placentæ placed equi-distant in pairs upon the face of each valve or carpel, and considerably

within the margin. In Epiphegus each carpel has two intramarginal placentæ, which diverge from the base upwards, and terminate before reaching the apex. In Lathræa there is to each valve but one placenta, which may be regarded as two confluent ones occupying the very face of the dorsal suture of the carpel. And finally, in Æginetia indica, and I believe in Æginetia abbreviata also, the placenta is in like manner confined to the axis of the valve, occupying the same position upon the carpels as in Lathræa, but broken up into a number of parallel plates of unequal depth, over the whole surface of which multitudes of minute seeds are distributed. If we connect these facts, about which there can be no sort of question, with the well-known placentation of Bixads (Flacourtiaceæ), Water Lilies (Nymphæaceæ), and Butomads, we shall find that they invalidate the general carpological rule, that the placentæ belong to the ventral suture of a carpel, and consequently alternate with the dorsal; and we shall have to admit that the position of the placentæ with regard to the margins of the carpel is reducible to no certain rule, but depends upon specific organisation. Consequently we shall no longer be unable to account for the unusual situation of the placentæ opposite the stigma, in Papaver (as M. Kunth has lately noticed), in Parnassia, or elsewhere.*

* The position of the placenta in Poppyworts (Papaveraceæ) has thus been explained by Mr. J. B. Howell:—"The simplest state of the capsule in the Papaveraceæ is exhibited by Bocconia, Linn., in which it consists of two dorsally-compressed carpels united by their margins, forming a flattened one-celled capsule containing a single seed, which is attached to the inferior part of the replum or annular receptacle formed by the united margins of the carpels, from which the greater portion of the latter separates in the form of valves. This annular receptacle is shown to be identical with true parietal placentas, although, except at a single point at its base, it does not bear ovules, by the latter being developed throughout its entire vertical extent on both sides the capsule in the cognate species, Macleaya cordata, Brown (Bocconia cordata, Linn.) The capsule is crowned by a deeply bifid stigma, whose internally plumose halves being widely reflexed correspond in situation and direction to their subjacent valves, and, therefore, alternate with the intervalvular parietal placentas.

It is interesting to remark, that in this, the simplest state of the structure of the capsule, the relation of parts exemplifies the law which expresses the necessary alternation of stigmas with parietal placentas; and that it is, therefore, the reverse of that exhibited by the more complex capsules.

In Macleaya cordata the two parietal placentas bear several ovules; and the lobes of the stigma, though capable of separation, are vertical and in close

We ought not indeed to be surprised at coming to this result; for if the ovules are, as botanists generally believe them to be, a modification of buds, then the uncertainty in the position of the placentary lines will only be conformable to the uncertainty in the origin of buds from leaves. If in

opposition, forming a furrowed stigmatic line, which necessarily corresponds to the placentas, and consequently alternates with the valves.

In Chelidonium the stigmatic lobes (which in Macleaya were capable of separation and complete reflexion) are more rigidly erect, but the furrowed line bears the same relation to the placentas, which now exhibit their bi-carpellary origin by bearing a double row of ovules.

In Glaucium, the stigmatic lobes become enlarged, but otherwise remain as in the last example. The parietal placentas are furnished with a linear spongy growth projecting from between the rows of ovules of each placenta, and uniting with that of the opposite side in the centre of the capsule, which is thus converted into two cells. This spongy dissepiment is usually described as arising from the extension of the placentas; an attentive examination at different periods of growth, however, will show that it is really distinct in structure though attached to them.

In Hunnemannia we have the first indication of an addition of parts; the stigma being obscurely four-lobed, indicating the manner in which new carpels, will, in other genera, become interposed between the two primary ones, which alone exist in the preceding instances.

In Eschscholtzia the additional stigmas (which are only indicated in Hunnemannia) are considerably developed, but are separate from the primary ones. The fact of their being the superadded stigmas is, however, indicated by their being shorter than the others.

In Meconopsis the additional carpels (only sketched forth and indicated, as it were, by the additional stigmas in Hunnemannia and Eschscholtzia) are perfected, each carpellary valve contributing by its margins to the formation of two parietal linear placentas, which latter correspond with the stigmatic rays. Each stigmatic ray is formed precisely similar to the stigma of Macleaya, Chelidonium, and Glaucium, being furnished with a central depressed line, indicating its formation from the union of the corresponding halves of the two contiguous carpels.

In Argemone the radiated stigma presents an undulatory folded appearance in consequence of the increased growth of the intervening tissue, which in the preceding genera (excepting Eschscholtzia) separates the lateral portions of the stigmatic extremity of each carpel.

We now arrive at Papaver, in the different species of which the capsule presents several states of complication by the successive addition of a greater number of carpels, which in P. somniferum sometimes amount to sixteen. The parietal placentas, which in all the preceding genera are linear, now project in towards the centre of the capsule, partially dividing it into as many imperfect cells. The stigmatic rays, which, as in the preceding instances, are equal in number to the placentas, and opposite to them, are, as already described, double, and only differ from those of Argemone in having the intervening tissue, which separates the two margins of the stigmatic extremity of each carpel, plane instead of folded." (*Annals of Natural History*, Vol. x.).

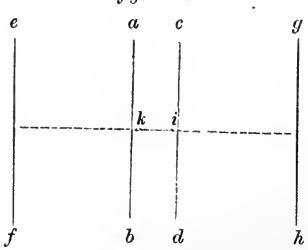
Bryophyllum, Malaxis paludosa, and most other cases, they usually spring from the edge of the leaf, they also arise from its surface in ferns; and in such cases as that of the Ornithogalum leaf mentioned by Turpin (*fig.* 19, p. 172) they were found issuing indiscriminately from all parts of its face.

When two leaves are developed upon a stem, they are always opposite, and never side by side. As carpels are modified leaves, they necessarily obey this law; and, consequently when a pair of carpels forms a bilocular ovarium, the separation of the two cells is directly across the axis of the flower.

The partitions in ovaries, that are formed by the united sides of cohering carpels, and which separate the inside into cells, are called *dissepiments* or *septa*. In order to form an exact idea of the structure of pistils, it is important to bear in mind, not only that such is really their origin, but that they cannot possibly have any other origin. Now, as each dissepiment is thus formed of two united sides, it necessarily consists of two plates, which are, in the ovary state, often so completely united, that their double origin is undiscoverable, but which frequently separate in the ripe pericarp. This happens in Rhododendron, Euphorbia, Pentstemon, and a multitude of other plants. The consideration of this circumstance leads to certain laws which cannot be subject to exception, but which are of great importance; the principal of which are these:—

1. *All dissepiments are vertical and never horizontal.*—For

fig. 128.

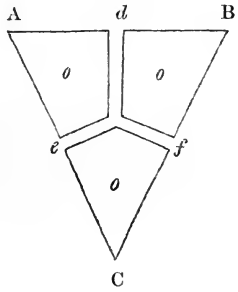


if *a b*, in *fig.* 128., represents the side of one carpel, and *c d*, that of another, the dissepiment *a c b d*, formed by this union,

will have precisely the same direction as that of the carpels, and can never acquire any other; and the same would be true of the sides *e f* and *g h*, if they formed themselves into dissepiments by uniting with other carpels: consequently a partition in any cell in the direction of *i k* could not be a dissepiment, but would be of a different nature.

2. *They are uniformly equal in number to the carpels out of which the pistillum is formed.*—Suppose the triangle A B C

fig. 129.



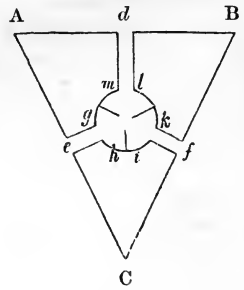
represented a transverse section of an ovary formed by the union of three carpels *o, o, o*; then *d, e, f* would be the dissepiments, and could not be either more or fewer in number.

3. *They proceed directly from the placenta, when that part originates in the margin of the carpel.*—As the placenta is then the margin of the carpellary leaf, and as the dissepiment is the side of the carpellary leaf, it is evident that in such a case a dissepiment cannot exist apart from the placenta. Hence, when any partition exists in an ovary and is not connected with the marginal placenta, it follows that such a partition is not a dissepiment, however much it may otherwise resemble one.

4. *They are alternate with placentæ formed by the cohesion of the margins of the same carpel, and opposite to placentæ formed by the cohesion of the contiguous margins of different carpels.*—Let the triangle A B C represent a transverse section of a three-celled ovary of which *d, e, f* are the dissepiments: the dissepiments *d* and *e* will alternate with the placentæ *m, g*, both belonging to the carpel A; but the dissepiment *d*

will be opposite the placentæ *m*, *l*, formed by the cohesion of the contiguous margins of the carpels A and B.

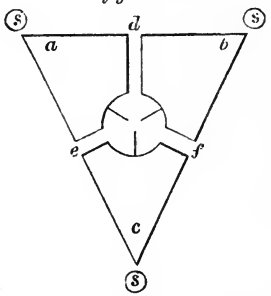
fig. 130.



5. *A single carpel can have no true dissepiment.*

6. *The dissepiment will alternate with the stigma* :—for the stigma is at the extremity of the carpellary leaf, or of the dorsal suture of the carpel; and the sides of either of these (which form dissepiments) will be right and left of the stigma, or in the same position with regard to the latter organ as the sides of the lamina of a leaf to its apex. Let the triangle *a b c*

fig. 131.



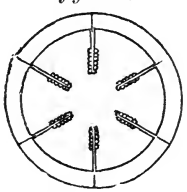
represent a transverse section of a three-celled ovary, of which *d*, *e*, *f* are the dissepiments. The stigmas would occupy a position equal to that of the spaces *s*, *s*, *s*, and would consequently be alternate with *d*, *e*, *f*, the dissepiments: they could not possibly be placed opposite *d*, *e*, *f*, upon any principle of structure with which we are acquainted. This law proves that neither the membrane which separates the two cells of a cruciferous siliqua, nor the vertical plate that

divides the ovary of Astragalus into two equal portions, are dissepiments: both must be expansions of some other part.

All partitions whose position is at variance with the foregoing laws are spurious. Such *spurious dissepiments* are caused by many circumstances, the chief of which are the following:—they are caused by expansions of the placenta, as in Crucifers, when they form a partition stretching from one side to the other of the fruit; or they are mere dilatations of the lining of the pericarp, as in Cathartocarpus Fistula, in which they are horizontal; or they are internal expansions of the dorsal or ventral suture, as in Amelanchier, Astragalus, and Thespesia, in which they are distinguishable from the dissepiments by not bearing the placentæ, and by being opposite the stigma, or by projecting beyond the placentæ; or, finally, they are caused by the sides of the ovary projecting into the cavity, uniting and forming many supernumerary cells, as in Diplophractum.

Such is the structure of an ovary in its most common state; certain deviations from it remain to be explained. We have seen that when carpels become syncarpous, they form a pistil whose ovary has as many cells and dissepiments as there are carpels employed in its construction. But sometimes the united sides of the carpels do not project so far into the cavity of the ovary as to meet in the axis; and then the result is an ovary, which, although composed of many carpels, is nevertheless one-celled (*fig.* 132.). In such case the disse-

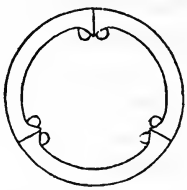
fig. 132.



piments project a short distance only beyond the inner lining, or *paries*, of the ovary, and bearing on their edges the placentæ, the latter are said to be parietal. In other plants,

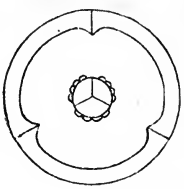
such as Corydalis, Viola, and Orchis, the carpels are not folded together at all, but are spread open and united by their edges (*fig.* 133.): in that case the placentæ do not project at all into the cavity of the ovary, but are still more strictly parietal than the last.

fig. 133.



Another class of anomalies, of a still more remarkable character, is that in which there are no dissepiments, while the placenta forms a distinct mass in the centre of the ovary, as in Lychnis; this is what is called a *free central placenta* (*fig.* 134.). The first explanation of this peculiarity was to

fig. 134.



refer it to the theory of universal sutural placentation, upon the supposition that in all such cases the dissepiments originally meet in the centre; but that subsequently the shell of the ovary grows more rapidly than the dissepiments, and breaks away from them; while the excessive growth of the placenta afterwards destroys almost all trace of the dissepiments: their previous presence being only detected by lines upon the shell of the ovary, or by the separation of the mass of ovules into distinct parcels upon the placenta.

Some years since it was thought that this was a perfectly satisfactory explanation of the free central placenta, and I, along with most other botanists, adopted that theory. But it is undoubtedly a mistake. This has been skilfully and

indisputably proved by Agardh, Schykoffsky, and Schleiden; the latter even maintains that in no cases is there any sutural production of ovules, or marginal placentæ, but that the placenta is a mere form of the growing point finally developed within the cavity of a carpel. Schleiden believes that the formation of the ovule in Taxus,—where it terminates a branch, and is naked, and where the leaves are arranged in the customary spiral direction, even to the extreme summit, and where no one leaf implies in the slightest degree an adaptation to the female part more than another,—is incompatible with the sutural theory; and he also adverts to the difficulty of explaining by it such a structure as that of Armeria, in which five carpels surround a single ovule, rising from the bottom of a cell upon a cord, which curves downwards at its apex, and thus suspends the ovule free in the centre of the cavity; he therefore supposes the ovule, and consequently the placenta, to be in all cases a production of the axis. The following is an extract from his valuable paper on this subject:—

"Although we cannot doubt that in plants possessing a free central placenta, or in those where, as in the Buckwheats (Polygonaceæ,) Taxus, Juglans, Myrica, the placenta cannot be supposed to exist as a separate organ, the nucleus of the ovule is only the summit of the axis, yet the question suggests itself as to how the parietal placenta is to be understood; and I do not consider the explanation to be very difficult. We find in many Arads that the axis is expanded at its summit into a kind of disk upon which is a number of buds or ovules, arranged like the flowers in the capitulum of Composites and other families. We next observe these disks expanded into lobed processes, and adherent to the edges of the carpellary leaves in all parietal or pseudocentral placenta; such a modification of the axis as this is what occurs in Dorstenia. The parietal placenta may be explained equally well, and perhaps with greater simplicity, as a mere ramification of the axis. It will not therefore surprise us that the buds or ovules of these branches grow only upon their inner side, viz. that side directed towards the axis; for the same is observed in the inflorescence of many plants, for instance, in Æsculus.

Lastly, in those plants in which the entire wall of the simple ovary is occupied with ovules, we find the axis expanded somewhat in the shape of a basin, as may also be seen in the similar modification of the stalk in many Roseworts (Rosaceæ) and in Figs.

"We find moreover in nature, that in parietal placentæ the edges of the leaves are never laid upon one another throughout their entire length, and so adhere to each other; but they become united from below upwards, by the subsequent growth of a more or less distinctly intermediate substance. This substance is very evident in Fumeworts (Fumariaceæ) and Crucifers, in which it appears much later than the carpellary leaves, stands exactly within them, and in the latter family forms the spurious partition, by its gradual extension towards the middle, and its subsequent adhesion. The placenta shows itself to be independent of the carpellary leaves, during its growth, most strikingly in the Abieteæ. My investigations of the earliest conditions of those plants have shown me that the organ which, since the researches of R. Brown, has been considered as an open ovarium, is only a scale-like expanded placenta: and that the organ which R. Brown has named bractea is the actual carpellary leaf. This result has been confirmed to me, in a most beautiful manner, by a cone of Pinus alba, which upon the upper half was covered with female, and upon the lower with male flowers. In the Abieteæ, the placenta, left without the least constraint, developes itself to such an extent, that at length the carpellary leaf itself appears as a mere supplementary part."

A translation of the earlier Russian Memoir of Schykoffsky has been published in the *Botanical Register*, for 1840; from which the following passage is extracted, to show the manner in which the matter is treated by this ingenious author:—

"It may appear to many almost enigmatical, why De Candolle, so zealous a searcher after truth, who from his numerous services to science, could not run the least risk of any taint to his fame by the recognition of a fault or of any partial views, should not have taken up Richard, who, in the 6th Brussels edition of his *Elemens de Botanique et de Physiologie végétale*, 1833, p. 136, says as follows: "Cette réunion,

cette soudure des deux bords opposés de la feuille carpellienne se fait constamment an moyen d'un corps intermédiaire composé de tissu cellulaire et de vaisseaux nourriciers, et qui tire son origine de la partie de la tige ou du pedoncule d'ou nait le carpelle; c'est sur cette partie seulement, et jamais sur le bord même de la feuille carpellienne que sont attachés les ovules ou rudimens des graines.' The cause of this apparent obstinacy of De Candolle and his whole school, lies, in my opinion, in this, that the party of his adversaries, not resting upon the general laws of organisation, nor on data furnished by nature, and not agreeing with the ruling theory as being merely an indeterminate obscure sensation, only repeat, in different words, almost the same thing which Linnæus and his followers had said a century before on the receptaculum proprium of the seeds; describing, if I may so express myself, ignorantly, the phenomena they observe, without investigating, so as to render complete, their organographic meaning. It is to the acute countryman of Linnæus, Agardh, late professor of botany at Lund, that the honour is due, on the one hand, of having pointed out the errors of De Candolle's theory, and on the other, of having applied to the flower and to the fruit the general law of vegetable organisation; according to which there always appears in the axilla of the leaf, a bud, or new shoot on which are developed, in their turn, leaves bearing again in their axillæ fresh buds.

"Thinking it out of place here to enter into any critical review of the small but acute composition of Agardh, published at Lund, in 1828, under the title of *Essai de réduire la Physiologie végétale à des Principes fondamentaux*, I shall only say, that according to Agardh's theory, the organ which bears the seeds is the representative of the branch or shoot springing from the axilla of the carpellary leaf.

"Under the guidance of Bacon's rule for the study of science, so especially applicable to the investigations of naturalists—'Malo Academiam ruminantem, quam quæ nova detegit,'—I applied myself, in the years 1831 and 1832, to the investigation of the structure of fruits and seeds. My intention was to ascertain how far facts bore out the theory of the learned Swede, derived merely from the general laws

of vegetation, as it were *à priori*, without adducing in support of it a single example taken from the observation of nature.

"To my no small satisfaction, I became, from day to day, more and more convinced, both from my own analyses and those of other accurate observers, of the correctness of Agardh's views; and, moreover, I saw that all those appearances which speak the most in favour of De Candolle's theory, can also, without effort or violence, be demonstrated according to the principles laid down by Agardh: for example, the apparent arrangement of the seeds on the two margins of the carpellary leaf at the opening of the pod of Leguminosæ, the frequent recurrence of an even number of ovules in simple polyspermous carpels, or in each cell of compound fruits, &c.; and that on the other hand all those appearances which after De Candolle's ideas can with difficulty, or as he himself admits, cannot at all be explained: for example, the attachment of the seeds in the fruit of Crucifers, the structure of Borageworts, Ochnads, Labiates, &c., become under Agardh's theory examples of the explanation of the appearance of the fruit of other natural families in the simplest and most satisfactory manner."

Duchartre has proved the truth of this theory by direct observation of development:—"At its first appearance the flower of the Primworts shows itself in the form of a small globule, a little depressed, and entirely cellular. In this state it is embraced by the young bract, the axil of which it occupies. Very soon, towards the base of the nascent bud, a slight peripherical and continuous swelling is seen, the free border of which is speedily crimpled into five little festoons. This swelling is the nascent calyx, and the five little processes the five organic sepals already soldered together. While the calycinal protuberance is making its appearance the young bud becomes a little enlarged, and five small rounded papillæ, alternating with the five sepals, are soon to be distinguished upon the upper part, now surrounded by the calyx. In a short time these papillæ become elevated, disengaged from the common base, and are to be distinguished as five small projecting bodies, rounded at the summit and sides, and slightly compressed within and without. These are easily recognised

as the five stamens alternating with the divisions of the calyx, and consequently opposite to those of the corolla.

"The bud, therefore, possesses in this young state two of its verticils, the calyx and the male apparatus. The latter is already clearly enough marked, while nothing yet indicates there the appearance of the corolla; but from the time when the stamens are developed into little distinct bodies, if the calyx be removed, a slight swelling will easily be distinguished at their origin, on the outer side, which swelling follows the whole outline of their common base, and forms a well-marked projection outside each of them. The slight swelling is the nascent corolla, and the five little projections opposite to the stamens are the five organic petals which compose it.

"About the time when the corollary protuberance shows itself on the exterior of the base of the young anthers, the female organ begins to manifest itself as a kind of continuous circular swelling, in the centre of which is perceived a small rounded papilla. The swelling is the first indication of the ovarian parietes, and the papilla the first sketch of the placenta. At this period the young pistil organises and developes its two portions equally.

"The peripheric swelling, rising more and more, quickly constitutes a kind of little utricle with rather thick walls, truncated and open at the summit, while the placenta, elongated and growing proportionally, forms a small ovoid body which exactly fills the cavity of this young ovary, but without exhibiting the slightest adhesion to its walls. In this state it resembles a young solitary ovule.

"A new modification now soon presents itself and becomes more and more marked. The little ovarian utricle contracts as it increases in length; thus its orifice in a short time becomes elevated to the summit of a little truncated cone, which is the commencement of the style. At the same time the young placenta is a little contracted towards its free extremity, so that its form is now turbinated, and its point generally fills up the inferior opening of the styliferous canal. Its surface, which until then had remained smooth, quickly swells into little rounded papillæ, which are the commencement of the ovules. These ovules in Dodecatheon,

Primula, and Cortusa, are numerous and arranged spirally." (See *Annals of Natural History*, xiv. 406.)

This evidence is irresistible, and has led to a more careful examination of the origin of the placenta, the result of which is, that, undoubtedly, in a very large number of cases, it is certainly an expansion or extension of the axis, and by no means a natural process. This is easily shown in Cranesbills (Geraniaceæ), Tutsans (Hypericaceæ), Bindweeds (Convolvulaceæ), Oxalids, Mallowworts, Myrtleblooms (Myrtaceæ), and many other natural orders. Brown, however, clings to the sutural theory :—

"I have assumed," he says, "that ovules belong to the transformed leaf or carpel, and are not derived from processes of the axis united with it, as several eminent botanists have lately supposed. That the placentæ and ovula really belong to the carpel alone is at least manifest in all cases where stamina are changed into pistilla. To such monstrosities I have long since referred, in my earliest observations on the type of the female organ in phænogamous plants, and since more particularly in my paper on Rafflesia: the most remarkable instances alluded to, in illustration of this point, being Sempervivum tectorum, Salix oleifolia, and Cochlearia Armoracia, in all of which every gradation between the perfect state of the anthera and its transformation into a complete pistillum, is occasionally found." This is, however, no answer to the evidence of Schleiden, Schykoffsky, and Duchartre; and has been thus disposed of by Link :—

"Such a general rule has always appeared to me, not merely doubtful, but altogether incorrect. For when do buds proceed from the margin of true leaves? A bundle of vessels never runs to the margin, whence buds or young shoots might proceed, and which would present the only analogy to the bundle of vessels, from which the ovules in the pericarp arise. If Bryophyllum calycinum be quoted, it serves for a reply, that the buds do not grow from the margin, but only in its neighbourhood, in the angle of the notch, where numerous delicate nerves interlace. Or, if Phyllanthus be adduced, we can easily reply, that here the so-called leaves are only expanded petioles, as the little scale below them

shows, which represents the real leaf. The supposition that the ovule originates from the midrib of a metamorphosed leaf is far more natural, and explains better the forms of the pericarp, if we only admit the inflection and slight coherence of the margins."

But it does not follow that, because the placenta has sometimes, it must always have, such an origin. We know that leaves do produce buds, we also know that the axis produces them; there is, therefore, no reason why the carpels, as well as the point of the axis which they enclose or surround, should not in like manner produce ovules. In fact, we have numerous cases of monsters, especially in Houseleeks (Crassulaceæ) and Crowfoots (Ranunculaceæ), in which the ovules do most certainly grow on the margins of leaves only partially converted into carpels. (See a remarkable example in *Elements of Botany*, p. 88. fig. 180.) Moreover, Dr. Grisebach, in his excellent *Genera et Species Gentianearum*, has shown that the placenta of that order cannot be an expansion of the axis, because the ovules are originally developed in two or three rows on the face of the carpels, forming a line of minute tumours from the base to half-way up the carpels; "quæ quidem series, parenchymate magis inter ovula quam in dorso *carpophylli* crescente, demùm ipsius superficiem ferè integram subæqualiter obtegunt."

The placentation of Water-lilies (Nymphæaceæ), Broomrapes (Orobanchaceæ), and Butomads, is equally at variance with the central theory; and, in their valuable paper upon the successive formation of the parts constituting the fructification of Leguminous plants, Schleiden and Vogel have clearly shown that in that case the carpellary leaf is originally a folded scale, and that when the ovules appear it is from the margins of that leaf, and not from the central point of the axis. (*Beiträge zur Entwickelungs-geschichte der Blüthentheile bei den Leguminosen.*)

The preceding theoretical views would seem to be in all respects satisfactory. It is, however, necessary to add that Dr. Robert Brown thinks that perhaps the structure both of ovary and anthers is not obviously reconcilable to any hypothesis hitherto proposed to account either for the origin

or for a common type of the sexual organs of Phænogamous plants. (*Linn. Trans.* xix. 225.)

12. Of the Receptacle.

The part upon which the carpels are seated is the apex of the peduncle, or the summit of the floral branch, of which the carpels are the termination. Usually this part, which is called the receptacle, is flat, or merely a vanishing point; but in other cases it is very much dilated, and then assumes a variety of curious appearances. This receptacle is called *torus*, or *thalamus* as well as *receptaculum*, and in Greek compounds has the name of *clinium*.

In Anonads and Magnoliads it elevates itself from the base of the calyx, and bears the numerous stamens peculiar to these orders; here it is called *gonophore* (gonophorum) by De Candolle. When it is succulent and much dilated, so as to resemble the receptacle of a Composite, bearing at the same time many ovaries, as in the Strawberry and Raspberry, Richard calls it *polyphore*: most commonly such a receptacle is sufficiently described by the adjective fleshy. If only a single row of carpels developes upon such a receptacle, as in Ochna, and there is an oblique inclination of the carpels towards the axis of the flower, we have the *gynobase* (Plate V. fig. 3. *a*); in the Geranium this part is remarkable for being lengthened into a tapering woody cone to which the styles adhere in the form of a beak; in Nelumbium it is excavated into a number of cavities, in which the ovaries are half-hidden. The receptacle is in reality the growing point of the flower bud, and is analogous to the spongy head of the spadix in Arum, and to the hard spines of the Blackthorn.

In all cases of central placentation the placenta is an extension of the receptacle, whose processes are introduced through the base of the carpels into their cavity, as has been shown by the evidence collected in the preceding pages.

In Cloveworts (Caryophyllaceæ) an internode below the receptacle is elongated, and bears on its summit the petals and stamens; De Candolle calls this *anthophore* (anthophorum.)

13. Of the Ovule.

The *Ovule* (Plate V. fig. 16. to 26.) is a small, semipellucid, pulpy body, borne by the placenta, and gradually changing into a seed. Its internal structure is difficult to determine, both in consequence of its minuteness, and of the extreme delicacy of its parts, which are easily torn and crushed by the dissecting knife. It is doubtless owing to this circumstance chiefly, that the anatomy of the ovule was almost unknown to botanists of the last century, and that it has only begun to be understood within ten or twelve years, during which it has received ample illustration from several skilful observers. Brown, indeed, claims to have pointed out its real nature so long ago as 1814; but the brief and incomplete terms then used by that gentleman, in the midst of a long description of a single species, in the Appendix to Captain Flinders's *Voyage,* unaccompanied as they were by any explanatory remarks, prove indeed that he knew something of the matter, but by no means entitle him to the credit of having, at that time, made the world acquainted with it. The late Mr. Thomas Smith seems to deserve the honour of having first made any *general* remarks upon the subject: of what extent they exactly were is not known, as his discoveries, in 1818, were communicated, as it would seem, in conversation only; but it is to be collected from Brown's statement that they were of a highly important nature. At a later period the structure of the ovule received much attention from Brown, in England; Turpin and Adolphe Brongniart, in France; and Treviranus, in Germany; by all of whom the subject was greatly illustrated. It was, however, to Mirbel,—who, by collecting the discoveries of others, examining their accuracy, and combining them with numerous observations of his own, first produced a full account of the gradual development and the different modifications of the ovule—that we were indebted for by far the best early description of this important organ. His two papers were read before the Academy of Sciences at Paris, in 1828 and 1829, and still deserve to be consulted notwithstanding some

errors and omissions which have since been corrected by the elaborate researches of Fritzsche, Schleiden, Griffith, Brown, and others.

Ovules have been compared to buds, and have been shown to be analogous to them in structure. This theory seems to be established by such plants as Bryophyllum, which habitually form buds on the margins of the leaves; or of Malaxis paludosa, in which the edge of the leaf is frosted by little microscopical points, that are neither exactly ovules nor exactly buds; or even by the bracts of Marcgraavia, which Turpin, with much ingenuity, has endeavoured by mere argumentation to prove analogous to the primine of the ovule. It has been shown by Henslow that in the Mignionette the ovules do actually become transformed into leaves, either solitary or rolled together round an axis, of which the nucleus is the termination. (*Cambr. Phil. Trans.* vol. v. part i.) Engelman, also, mentions and figures instances of similar changes; but he does not say in what plants, nor are his figures satisfactory. He, however, concludes, from the observations of himself and Schimper, that "the ovules are buds of a higher order, their integuments leaves, and their stalk the axis; all which, in cases of retrograde metamorphosis, are converted into stem and green leaves." (*De Antholysi Prodromus*, § 44. 76. t. 5. f. 4, 5.) One would rather say that the evidence goes to prove the ovule to be a leaf-bud in a particular state, the integuments to be scales (*i. e.* rudimentary leaves) rolled up and united at their touching margins, and the nucleus to be the growing point, to which I have already on so many different occasions directed attention.

The correctness of this view has been maintained by Dr. Giraud who regards it as being "established on the following grounds. The primine and secundine, at a very early period of their development, are not presented each as a continuous membrane encircling the nucleus, but they consist of several portions, forming two whorls of what I would term ovular leaves, their internode being wanting; its normal position being occupied by a portion of tissue near

the chalaza. This opinion is also supported by the instances which have been noticed of the descending metamorphosis of the ovule. MM. Henry and Marquart have noticed the retrograde or descending metamorphosis in the ovules of the Salix cinerea, and have represented, in drawing, a catkin, the carpels of which were filled with a number of longitudinally folded leaves occupying the normal situation of the ovules; doubtless these were the organs which should have constituted the ovular membranes. Hence, then, it may be concluded that the axis has its termination at some point within the ovule; this I would consider to be situated at the chalaza; here, the vessels which have ascended through the woody tissues of the stem, and have penetrated the cellular structure of the placenta, are suddenly stopped, as it were, in their course, and are spread out in ramifications to the nucleus and its tegumentary membranes; thus forming the true organic placenta."

It is, however, to be remarked that if the ovule is really a leaf-bud, (the last which the axis of growth is capable of producing) its integuments are not formed in the same order as leaf-bud scales. In a leaf-bud of two scales the outer forms first, then the second, and within the second the growing point. But in an ovule the growing point, if the nucleus be it, appears first, then the interior integument, and afterwards the exterior. It is, moreover, not to be forgotten that in the monstrous Aquilegia figured in the *Elements of Botany*, p. 88. t. 180, each ovule actually grows into a *true leaf*, and not a leaf-bud, the nucleus being the apex of the leaf. This does not seem quite consistent with the theory that ovules are leaf-buds; and further evidence must be sought before the question can be regarded as settled.

In almost all cases the ovule is enclosed within an ovary, as would necessarily happen in consequence of the convolute nature of the carpellary leaves: but if the convolution is imperfect, as in Reseda, the ovules are partially naked; and if it does not exist at all, as in Cycads and Conifers, the ovules are then entirely naked, as was first shown by Brown, and, instead of being fertilised by matter conveyed through the

stigma and the style, as in other plants, are exposed to the direct influence of the pollen.

The occurrence of a naked ovule has been asserted by Schleiden to take place in Viscum; but Mr. Griffith has pointed out this error in the *Linnæan Transactions* (vol. xix.), and refers the appearance to what has been termed a solid ovary, upon the evidence of M. Decaisne, on Viscum album, and that derivable from some casual observations made by himself in 1838 on a Himalayan species of the same genus. But he has shown this to have been a mistake; and he in his last paper declares that there is, perhaps, nothing more constant than the existence of a cavity in the pistil, nor is its absence compatible with the rule, that a pistil is formed from one or more involute carpellary leaves. "It is easy," says Mr. Griffith, "to conceive a pistil without any very manifest cavity; for the space, which must exist from the disposition of its component parts, may be filled by an extension of the placenta, or the margins of the laminæ of those component parts, and indeed by several other modes of extension of its inner surface. But the solidity which I prematurely announced as existing in Loranthus, was of a very different nature, and could not be reconciled to that idea of a pistil, which I have been led to adopt. The anomalies of the mere pistil of Loranthus I at present consider to be confined to the obscurity of the cavity, particularly as connected with obscurity of the placenta. I have, however, seen in Loranthus bicolor appearances which lead me to suspect that much still remains to be observed, not only as regards the conical eminence from the fundus of the cavity, but as regards the true limits of the ovarium. I have not been able to find any such ovarial cavity in two species of Viscum I have lately examined; but I almost feel convinced, that an obscure ovarial cavity similar to that of Loranthus does exist; for, in addition to the strong doubts that must arise from any apparent infraction of a general law, M. Schleiden has stated that in Viscum album there is a nucleus, and consequently an ovarial cavity. The late appearance of the ovule does not, I think, present so remarkable an anomaly as the solidity of the ovarium, unless it can be shown that the development of

the ovule results from the action of the pollen. For there are many instances of considerable irregularity in the degree of development of the ovule at the period of expansion of the flower. From M. Decaisne's description of the ovule of Viscum album, which appears to agree tolerably well with that of an Himalayan species, it is, I think, evident that in the earlier stages of its development it may defy observation, since at one period it would seem to consist of nothing but a single cell, scarcely, if at all, distinguishable from the cells composing the surrounding cellular tissue."

When the ovules are attached to the placenta by a kind of cord, that cord is called the *funiculus* (Plate V. fig. 26. *a*), and is a prolongation of the placenta.

In the beginning the ovule is a pulpy excrescence (Plate V. fig. 16.), appearing to be perfectly homogeneous, with no trace of perforation or of envelopes. But, as it advances in growth, it is gradually (Plate V. fig. 17. to 21.) enclosed in one or two sacs or integuments, which are open only at their apex, where, in both these sacs, a passage exists, called the *foramen* (Plate V. fig. 21. *a*); or, in the language of Mirbel, *exostome* (fig. 25. *a*) in the outer integument, and *endostome* (fig. 25. *b*) in the inner integument. The central part is a fleshy, pointed, pulpy mass, called the *nucleus* (Plate V. fig. 19, 20. *a*, 22. *b*, 23. *c*, 24. *d*, 25. *e*, 27. *e*).

The outermost of the sacs (Plate V. fig. 22. *c*, 23. *a*, 25. *c*) is called the *primine*. It is either merely a cellular coating, or it is eventually traversed by veins: these are sometimes very apparent, as in Citronworts (Aurantiaceæ), and Mirbel seems disposed to think that they often exist in a rudimentary state when they are not visible. Usually it is nearly as long as the secundine, but sometimes it is remarkably shorter, as in Euphorbia Lathyris when very young (Plate V. fig. 22.)

The outermost but one of the sacs (Plate V. fig. 23. *b*, 20. *b*, 25. *d*) is called the *secundine*; it immediately reposes upon the primine, and sometimes contracts an adhesion with it, so that the two integuments become confounded. In order to ascertain its existence, it is, therefore, necessary to examine the ovule at a very early period of its growth.

Myrica, Alnus, Corylus, Quercus, and Juglans have been named by Mirbel as plants in which the secundine is not perceptible (Plate V. fig. 24). Its point is usually protruded beyond the foramen of the primine.

The *nucleus* (Plate V. fig. 22. *b*, 18, 19, 20. *a*, 24. *d*, 25. *e*) is a pulpy conical mass, enclosed by the primine and secundine, and often covered by them; but frequently protruded beyond the latter, and afterwards, at a subsequent period of its growth, again covered by them. Sometimes its epidermis is said to separate in the form of a third coating called the *tercine*. It always contains an *amniotic sac*.

The *sac of the amnios* is a cavity filled with fluid, lying in the interior of the nucleus. It is the *vesicula amnios* of Malpighi, the *sac of the embryo* or *amniotic sac* of others, the *additional membrane* of Brown, the *quintine* of Mirbel. The latter author originally described it thus:—

"At the centre of the tissue is organised, as in a womb, the first rudiment of the quintine; it is a sort of delicate intestine, which holds by one end to the summit of the nucleus, and by the other end to the chalaza. The quintine swells from top to bottom; it forces back on all sides the tissue that surrounds it, and it often even invades the place occupied by the quartine or the nucleus. A very delicate thread, the *suspensor* * (*hypostasis* of Dutrochet), descends from the summit of the ovule into the quintine, and bears at its extremity a globule which is the nascent embryo."

The fluid matter contained within the nucleus is called the *liquor amnios*, and is supposed to be what nourishes the embryo during its growth.

"There appears to be little," says Mr. Griffith, "definite about the sac of the embryo, either in period of development, situation, or structure: but ordinarily it may be recognised

* It is this suspensor that Brown describes, in the ovule of Orchids, as a thread consisting of a simple series of short cells, the lowermost joint or cell of which is probably the original state of what afterwards, from enlargement and deposit of granular matter, becomes the opaque speck, or rudiment of the future embryo. (*Observ. on the Organs, &c., of Orch. and Asclepiad.* pp. 18, 19.) For further information concerning the suspensor, see Mr. Griffith's observations in the chapter on FERTILISATION in Book II.

as the sac existing within the nucleus, and as that in which the embryo is developed. I know of no positive character that can be assigned to it; for I have reason to believe that in Xanthium a second sac is to be found; and to say nothing of it, Osyris shows that the embryo is occasionally developed outside it. Very generally it is confined to the nucleus. (See the observations upon the *aril* at a future page).

The primine, secundine, and nucleus, have all an organic connection at some one point of their surface. That point is, in ovules whose parts do not undergo any alteration of direction in the course of their growth, at the base next the placenta; so that the nucleus is like a cone, growing from the base of a cup, the base of which is connected with the hilum through another cup like itself (Plate V. fig. 23.). The axis of such an ovule, which Mirbel calls *orthotropal*, is rectilinear, as in Myrica, Cistus, Urtica, &c.; and the foramen is at the end of the ovule most remote from the hilum.

But sometimes, while the base of the nucleus and that of the outer sacs continue contiguous to the hilum, the axis of the ovule, instead of remaining rectilinear, is curved down upon itself (Plate V. fig. 26, 27.); so that the foramen, instead of being at the extremity of the ovule most remote from the hilum, is brought almost into contact with it. Examples of this are found in Cloveworts (Caryophyllaceæ), Mignionette, &c. Mirbel, who first distinguished these ovules, calls them *campylotropal*. In both these modifications, the base of the ovule and the base of the nucleus are the same.

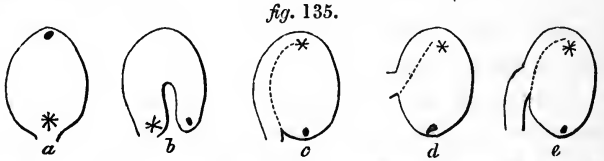
In a third class the axis of the ovule remains rectilinear; but one of the sides grows rapidly, while the opposite side does not grow at all, so that the point of the ovule is gradually pushed round to the base; while the base of the nucleus is removed from the hilum to the opposite extremity (Plate V. fig. 16—21.): and when this process is completed the whole of the inside of the ovule is reversed; so that the apex of the nucleus, and consequently the foramen, correspond with the base of the ovule. Such ovules as these Mirbel terms *anatropal*; they are very common: examples may be found in the Almond, the Apple, the Ranunculus, the Cucumber, &c. When the base of the nucleus is thus removed from the base

of the ovule, a communication between the two is always maintained by means of a vascular cord, called the *raphe* (Plate V. fig. 24. *e*, 25.*f*). This raphe, which originates in the placenta, runs up one side of the ovule, until it reaches the base of the nucleus: and there it expands into a vascular disk or plate, which is called the *chalaza* (Plate V. fig. 24. *f*. 25. *g*). As the chalaza is uniformly at the base of the nucleus, it will follow that, in orthotropal and campylotropal ovules, it is confounded with the hilum; while it is only distinguished in anatropal ones, in which alone it is distinctly to be recognised.

In addition to these there is the *amphitropal* ovule, whose foraminal and chalazal ends are transverse with respect to the hilum, which is connected with the latter by a short raphe; and the *semianatropal*, which is only different from the last, in the ovule being parallel with the funiculus instead of being at right angles with it.

The following figures give a comparative plan of these ovules:—

fig. 135.



a, Orthotropal, or atropal; *b*, campylotropal; *c*, anatropal; *d*, amphitropal; *e*, semianatropal. In these figures * represents the chalaza, and ' the foramen.

When an ovule grows erect from the base of the ovary, it is called *erect;* when from a little above the base, *ascending;* when it hangs from the summit of the cavity, it is *pendulous;* and when from a little below the summit, it is *suspended.*

It has been remarked that the raphe or vascular extension of the placenta always occupies the side next the ventral suture of the ovary; and that when, as in Euonymus, it is turned towards the dorsal suture, that circumstance arises from an alteration in the position of the ovule subsequent to its being fertilised.

This curious fact has been capitally illustrated by Schleiden: "Robert Brown," says this writer, "struck by finding in the

same genus (Euonymus) both pendent and erect ovules at the same time, investigated the history of the circumstance and thus discovered the law, that the raphe invariably passes, along the side of the ovule, turned towards the placenta; that in the pendulous ovules of Euonymus this is not the case, but that they become erect ovules, if we suppose the raphe to be brought into the right position; and that, therefore, the ovules of this plant are only curved downwards, having been, in reality, erect. The correctness of this statement is confirmed by tracing the development of the parts. Crowfoots (Ranunculaceæ) offer some remarkable examples of the same kind. The one-seeded plants of this family have been divided by the difference of pendent and erect ovules into Ranunculeæ and Anemoneæ; and botanists have imagined so important a distinction really to exist, even between plants so nearly allied to each other. But in these two divisions of Crowfoots the ovule is, when young, exactly the same, being ascending and anatropal. At a subsequent period the ovary either grows exclusively at its point, when we have an erect anatropal ovule, or the ovary expands downwards below the ovule, which then curves from the placenta downwards and becomes spuriously pendulous and anatropal with the raphe turned from the placenta. In several cases no difference is perceptible at the time of flowering (for instance between Ranunculus and Myosurus); and in others the intermediate states run so gradually together, that the difference alluded to is wholly unfit to be made a ground of division. But when the seeds are ripe it really does afford a well-defined distinctive character."

It has also been stated that the passage through the primine and secundine is called the foramen; or the exostome, when speaking of that of the primine; and the endostome, in speaking of the secundine. Upon these Mirbel remarks:— "These two orifices are at first very minute, but they gradually enlarge; and, when they have arrived at the maximum of dilatation they can attain, they contract and close up. This maximum of dilatation is so considerable in a great number of species, in proportion to the size of the ovule,

that, to give an exact idea of it, I would compare it not to a hole, as those express themselves who have hitherto spoken of the exostome and endostome, but to the mouth of a goblet or of a cup. It may therefore be easily understood, that, to perceive either the secundine or the nucleus, it is not necessary to have recourse to anatomy. I have often seen, most distinctly, the primine and secundine forming two large cups, one of which encompassed the other without entirely covering it, and the nucleus extending itself in the form of an elongated cone beyond the secundine, to the bottom of which its base was fixed."

In practical botany the detection of the foramen is often a matter of great importance; for it enables an observer to judge from the ovule of the direction of the radicle of the future embryo: it having been ascertained by many observations that the radicle of the embryo is almost always pointed to the foramen. A partial exception to this law exists, however, in Spurgeworts (Euphorbiaceæ), in many of which Mirbel has noticed that, after fertilisation, the axis of the nucleus and the endostome are inclined five or six degrees, without the exostome changing its position; by this circumstance the foramen of the secundine and that of the primine cease to correspond, and the radicle, instead of pointing when formed to the exostome, is directed to a point a short distance on one side of it.

Mr. Griffith has pointed out an example of departure from this law, in Cryptocoryne ciliaris (*Linnæan Transactions*, vol. xx). This exception, however, he regards as being corroborative of the validity of the law, since in the earlier periods of development the direction of the embryo is not only rectilinear, but the radicle corresponds exactly with the apex of the nucleus, and with the foramen. He would limit the expression of the law to "radicle pointing or corresponding to the apex of the nucleus," since there are exceptions to its correspondence with the foramen. "Another circumstance is likewise to be kept in view, viz. that the law is applicable only to the direction of radicles of embryos, which remain inclosed in the original nucleus, or in some modification of its original form."

Gasparrini also states, that in the seeds of the common China Orange (Citrus Bigaradia sinensis) there are several embryos, which are different from each other both in form and situation. Usually their radicle is turned to the foramen, sometimes it is entangled in the sides of the inner skin, and occasionally, but rarely, embryos are to be found *with the radicle turned to the chalaza.* This very curious and unexpected observation I have not been able to verify.

Besides the two external integuments, Mirbel remarked the occasional presence of three others peculiar to the nucleus, which he calls the *tercine, quartine,* and *quintine.* These terms are now, however, disused, and arose from imperfect observations. The tercine was the surface of the nucleus; the quartine a layer of tissue belonging to the tercine, and the quintine what is now called the *sac of the amnios.*

Recent investigations show that the number of integuments or sacs found on ovules never exceeds two, is frequently only one, that not uncommonly the nucleus is naked, and that there are even examples of an ovule consisting of no more than an amniotic sac.

It has been stated by Fritzche in Wiegmann's *Archiv.*, that, in many plants, the ovule has but one integument, as in Conifers, Composites, Lobeliads, Gentianworts, &c.; and in others two, as in Buckwheats, Rockroses (Cistaceæ), Urticals, Arads, and all other endogens, &c. He moreover found that while all endogens have two integuments of the ovule, the majority of monopetalous exogens have but one, whilst the polypetalous usually possess two.

Schleiden has, however, shown that the number of integuments of the ovule, varies in Crowfoots (Ranunculaceæ), even in the same genus. There is but one integument in Thalictrum, Anemone, Ranunculus, Caltha, Helleborus, some Delphiniums, and Podophyllum. Two integuments, he says, occur in Clematis, Adonis, Trollius, Isopyrum, Aquilegia, Aconitum, Pæonia, several Delphiniums, and also among Magnoliads. So great, he adds, is the difficulty of examining most plants of this family with reference to the original structure of their ovule, that possibly some error may

have crept into the preceding enumeration (perhaps in Delphinium). But even if it is only correct in the main, the conclusion is inevitable—that the number of ovular integuments, though constant in most other families, is among Crowfoots, a variable and consequently secondary character, by means of which alone the natural order cannot be limited. He finds similar anomalies among Arads, where there is nothing constant in the formation of the ovule, except the double integument of all monocotyledons. (See *Annals of Natural History*, v. 165.)

The reduction of the ovule to a mere nucleus has been treated of by Mr. Griffith, in his memoir on the ovule of Santalum, &c.:—

"The non-development of either of the ordinary integuments of the ovulum, that is, the reduction of this to the nucleus, was, so far as I know, first observed by M. Adolphe Brongniart in Thesium; and this is the only point on which the observations of that distinguished botanist agree with the later ones of M. Decaisne. This sort of reduction or suppression is now known not to be uncommon; it is usually, I believe, considered to be limited to antitropal ovula; but from the consideration of Galium, Callipeltis and Osyris, I am inclined to believe that changes in direction affect nucleary ovula similar to those affecting more complete ovula, so permanently established by M. Mirbel. This suppression having first been made manifest in Santalaceæ, it naturally became a subject of consideration whether it did not exist in similar placentations of certain other natural families, of which Olacineæ, certain Verbenaceæ and Avicennia are marked examples. On this subject my direct observations are confined to Congea; and although these are incomplete, I am led to believe that there is not any connexion between this mode of placentation and this mode of suppression. It is curious, however, that the ovula of the above instances, so far as I am acquainted with them, simulate at the period of expansion of the flower in a sufficiently marked manner the ovula of Santalaceæ." (*Linnæan Transactions*, xix. 185.)

The reduction of the ovule to little more than an amniotic sac was remarked by the same great observer who showed

that the ovule of Santalum album consists of nothing more than a naked nucleus, from within the apex of which the sac of the amnios *protrudes in the form of a long tubular process.* The same excellent botanist considered it probable that it will hereafter appear that the sac of the amnios is the only essential part of an ovule. (*Linnæan Transactions,* xviii. 77.) These observations were followed by others on the part of M. Decaisne, who found that in Thesium the structure of the ovule is of the same nature as that of Santalum. (*Comptes rendus,* viii. 203.)

The history and functions of this embryonic sac are so curious and important that I find it necessary to give Mr. Griffith's views at some length, although greatly abridged, from his elaborate paper in the *Linnæan Transactions* :—

"The first protrusion of the amniotic sac beyond the apex of the nucleus takes place long before the opening of the flowers or anthers; at the earliest period it presents itself as a membranous tube of nearly equal diameter, the exserted part being rather longer than the ovule; and the included part apparently originating from the base of the ovule, beyond which it does not appear to be extended posteriorly.

When the flower-bud is half developed, the embryo-sacs will be generally found to have attained nearly their full length in regard to the outside of the placenta; and with reference to the inside of this organ, they have undergone a remarkable modification, consisting in their extension backwards and upwards, beyond the base of the ovule towards the axis of the placentæ. The apex of the sac appears up to this period to be quite simple. An enlargement of the part near the apex of the nucleus has commenced, and is called the bulb or bulbous portion.

The changes that occur in the sac, prior to fecundation, consist in the deflection of the posterior extension of the sac in the direction of the axis of the placenta, and in the appearance of cellularity and division of the apex. The contents likewise appear to undergo some changes; but these are limited to the apex, and seem to consist of a sort of condensation, and irregular and variable division, of the grumous matter. At the period of expansion of the flower, the posterior

extensions will be found to have reached nearly to the base of the placenta. Their terminations in this direction are in culs de sac; there is a tendency to division and irregularity of outline of all the included part, not even excepting that within the ovule itself. The contents seem, with the exception of the part within the ovule, to be chiefly grumous matter." A similar structure was observed in other plants. In Osyris the ovule is reduced to a nucleus and embryonary sac, which is prolonged in the same directions as in Santalum, but not to such a degree beyond the apex of the nucleus. In Viscum the modifications appear to be two: in the one an evident cavity exists in the ovary, and the ovule seems to be reduced to an embryonary sac hanging from one side of the base of a nipple-shaped or conical placenta. In the other the ovule is reduced to an embryonary sac, but this is erect, and has no such obviously distinct point of origin as in the first. The gradation of structure appears to be tolerably complete. One modification of Viscum, in the opinion of Mr. Griffith, tends to show that in Santalum the first steps towards the disappearance of the usual nucleus take place; Osyris seems to indicate that a similar tendency may affect the embryonary sac; and Santalum appears to allude to a reduction in the embryo sac to the form of that of Osyris.

The manner in which the ovule is gradually developed has been frequently described, but by no one with more exactness than by Brown in Rafflesia. This botanist says:—

"The first perceptible change taking place in the papilla (which all ovules resemble at their earliest appearance) is a slight contraction at its summit, the upper minute contracted apex being the rudiment of the nucleus. Immediately below this contracted portion a dilatation is soon observable, which, gradually enlarging and becoming slightly hollowed, forms a cup in which the nucleus, also proportionally increased in size, is partly immersed. This cup, the rudiment of the future integument, continues gradually to enlarge, until it completely covers and extends considerably beyond the nucleus, but without cohering with it. If a

transverse section is made near the slightly-depressed apex of this integument, an extremely minute perforation or capillary channel, extending to the free apex of the included nucleus, may be observed. This account of the gradual development of the ovulum of Rafflesia, I believe, is in every essential point applicable to Phænogamous plants generally, except that here one coat only is developed. It is, however, in some important points different from the description given by M. Mirbel, who considers the nucleus in its earliest state as included in the integuments, which in the next stage open and dilate so as to leave it entirely exposed; they then, as he supposes, remain quiescent until the nucleus has considerably enlarged, when they again become active and increase in size until they once more completely cover it. While the development, as I have here described it, of the nucleus and its integuments in Rafflesia is going on, another change is at the same time gradually taking place, namely, at first a slight bending, which at last ends in a complete inversion, in the direction of the nucleus and its integument in regard to the placenta, with which, in this advanced stage, the perforated apex of the latter is nearly or absolutely in contact. In this change of direction, the ovulum of Rafflesia resembles that of the far greater part of Phænogamous plants: the change, however, is effected in a way which is much less common, the curvature in Rafflesia taking place solely in the upper part of the funiculus, the direction of the inverted ovulum being parallel with, but distinct from, the portion below the curvature; whereas in Phænogamous plants generally, the curvature is produced in that part of the funiculus which is connate with the testa or outer integument. For this difference a reason, perhaps, may be assigned; the integument which generally forms the testa or outer coat being in Rafflesia entirely wanting, or only indicated by the remarkable dilatation of the apex of the funiculus." (*Linn. Trans.*, xix. 225.)

Schleiden's account of the progressive growth of the atropal ovule in Buckwheats (Polygonaceæ), shows the same phenomena:—"At a certain distance below the apex of the original protuberance (Brown's papilla) an ideal line may be recog-

nised, intended as the basis of the nucleus, which does not afterwards increase in thickness. Above this line the apex forms itself into the nucleus, and below it the substance of the axis expands and forms a protuberance, which extending itself as a kind of membranous fold gradually covers in the nucleus (*Integumentum primum aut internum,* mihi; *Secundine,* Mirb.; *Membrana interna,* Auct.) Sometimes soon after, and indeed almost contemporaneously with this, sometimes later, sometimes immediately below the first protuberance, at other times at some distance from it, as, for instance, in many Buckwheats (Polygonaceæ) and Rockroses (Cistaceæ), we may next observe a second protuberance, which, as the second integument, covers in the first (*Integumentum secundum sive externum,* mihi; *Primine,* Mirb.; *Testa,* Auct.). The first-formed integument certainly does frequently consist only of a fold of the epidermis of the nucleus; nevertheless, we find a tolerably thick parenchyma taking part in its formation in almost all those families which form no second integument, and also in some which possess both coverings, as, for instance, in Spurgeworts (Euphorbiaceæ), Rockroses and Daphnads (Thymelaceæ)."

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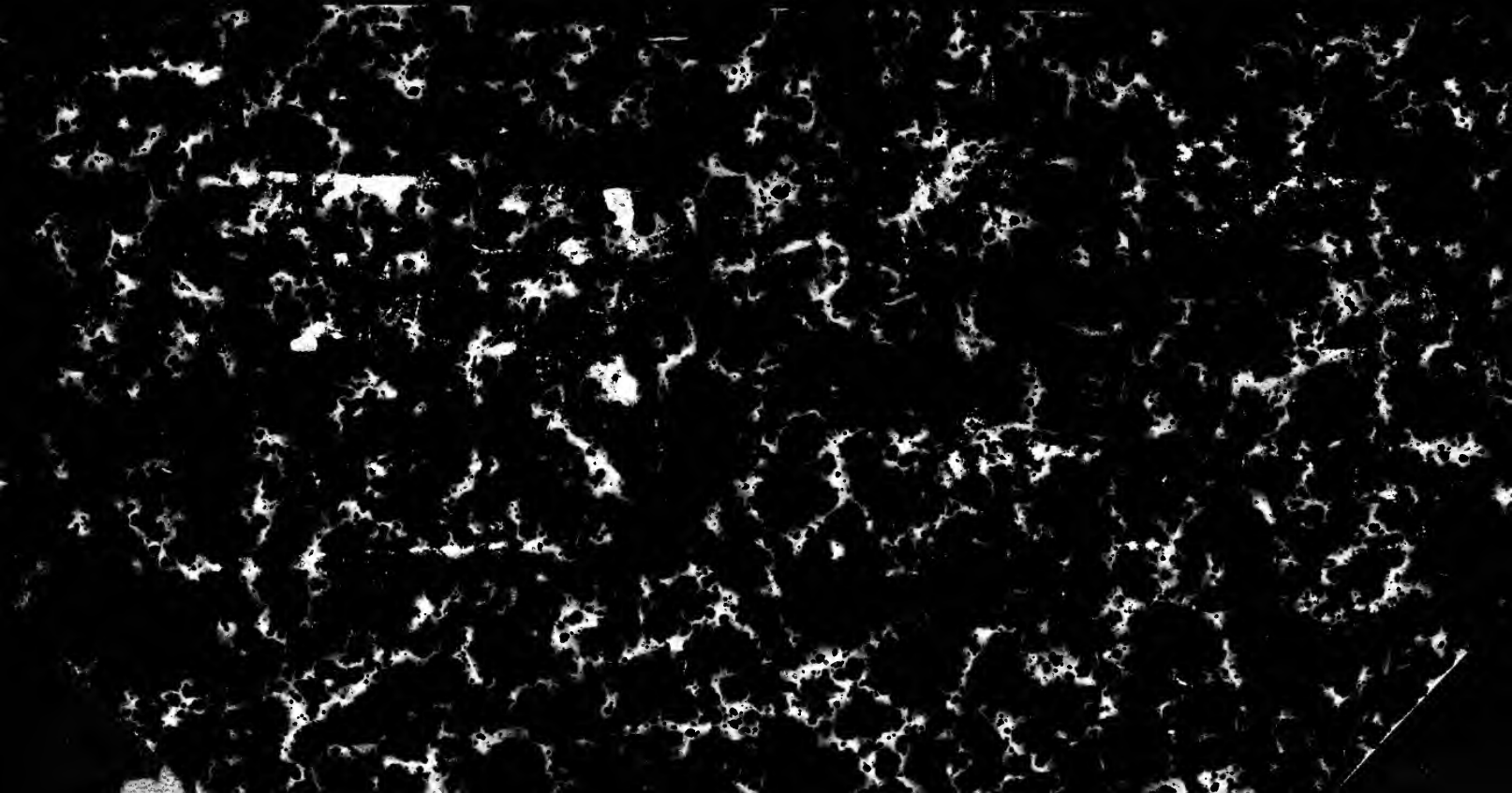
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